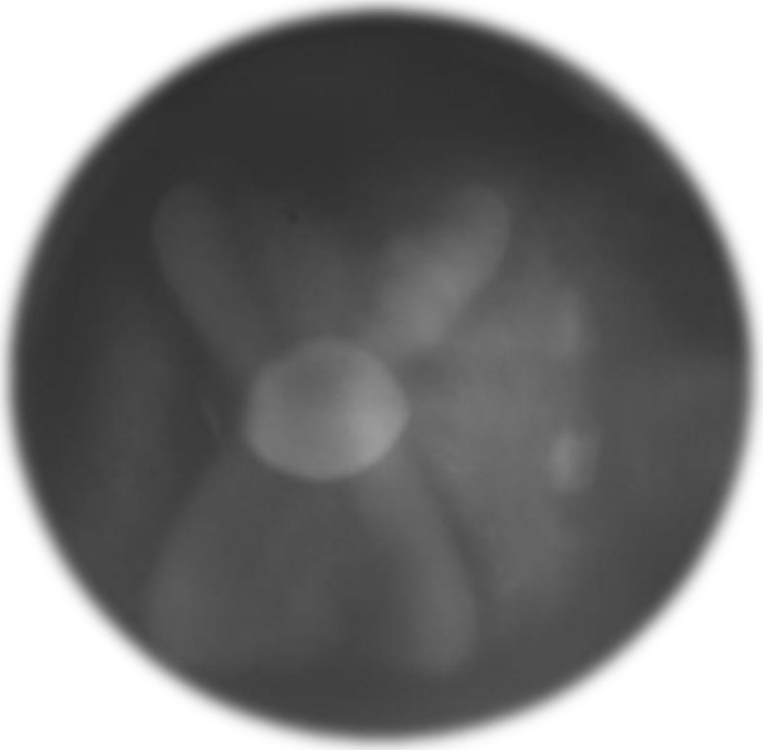
The Effect of Visual Priming in Jumping Spiders



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Abstract

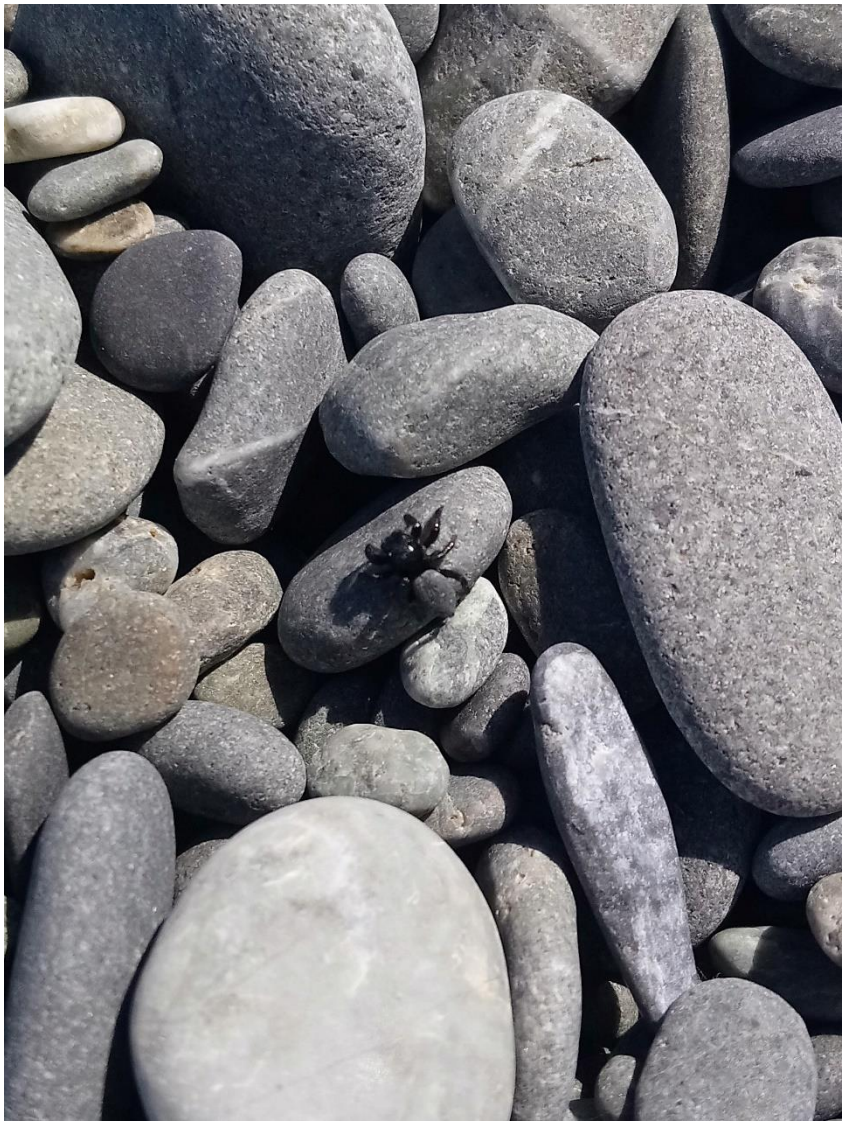
Priming of an animal's sensory system can influence behaviour. Once an animal has been primed with a stimulus (e.g., the smell of a specific prey), it is then able to find the source of the stimulus (e.g., visually locate the prey) more easily than before. Visual priming has been most extensively studied in birds, yet jumping spiders (Salticidae) are ideal for studies of visual priming. Being extremely visual, salticids have a wide range of complex, visually-mediated behaviours.

Salticids have a unique, distributed visual system consisting of a pair of large primary eyes which are used for high spatial acuity and colour vision, and three sets of smaller, secondary eyes used for motion detection. While the primary eyes are responsible for object recognition, the resolution of the secondary eyes is also good enough to support visually-mediated behaviour. Combined, the four pairs of eyes give the spider a 360° field of view. This unique system is responsible for salticids having the highest spatial acuity for their body size of any animal. The aim of this study was to determine whether priming of the secondary eyes influences the scanning response of the primary eyes in the salticid *Marpissa marina.*

A specialised eye-tracker was used to simultaneously present visual stimuli to the spider while recording the response of the primary eyes. The secondary eyes of the jumping spider were primed with a stimulus (circle or bar) that either matched or mismatched a stimulus later presented to the primary eyes. Analyses of the scanning patterns and scanning activity of the primary eyes indicates that visual priming is occurring within the salticid visual system. This is the first evidence of visual priming happening within the distributed visual system of a salticid. By facilitating the scanning patterns of the primary eyes, priming from the secondary eyes is likely to cause salticids to make faster and more accurate decisions in nature.

Chapter 1:

Introduction



Adult female *Marpissa marina* in natural habitat (Photo: L. Scott)

Introduction

Many animals use vision to gain information about their environment (Land 1981, Hayhoe and Ballard 2005). As a result, eyes have evolved multiple times within the animal kingdom (Nilsson 2013). While numerous animals have good vision, not all eyes are made equally and vision varies significantly between species (Jackson et al. 2006a). Compound eyes are made up of thousands of individual lenses, each with their own photoreceptor units (ommatidia); the image seen by the animal consists of the inputs from all ommatidia combined. Therefore, compound eyes have limited resolution capacities and will always have a lower spatial acuity than camera-type eyes (Land 1997). Spatial acuity is the visual resolution of an eye and is defined as "the minimum separation required before objects in the environment are seen as separate" (Harland et al. 2012). Compound eyes have a resolution around 1000 times worse than a human eye (Chittka and Spaethe 2007). Consequently, for a compound eye to have the same acuity as a human eye, the eye would need to have a radius of around six meters (Land 1997). Camera-type eyes, possessed by most vertebrates including humans, eyes have a single lens, which focuses the image onto a retina; which allows for greater spatial acuity than a compound eye of the same size.

Humans are highly visual animals with exceptional vision. The human visual system is extremely fast and efficient at obtaining information; humans can visually identify a scene containing an animal in as little as 120 ms (Kirchner and Thorpe 2006). Being highly visual, we are able to intuitively understand how the visual systems of other animals operate and how they can mediate certain behaviours; as a result, animal visual systems are some of the most well-studied sensory systems (Sanes and Zipursky 2010).

Invertebrates are ideal organisms for studying vision, as they can be easily manipulated and live in hugely diverse environments (Briscoe and Chittka 2001). In particular, spiders are model organisms for the study of vision (Cross and Jackson 2009). Spiders are among the most diverse groups of animals on Earth (Coddington and Levi 1991) and occupy almost all terrestrial habitats on every continent except Antarctica (Jackson and Hallas 1986). Spiders may initially be considered an unusual choice of animal for studying vision, as most web-building spiders are deemed to have poor vision which plays only a minor role in their behaviour (Hu et al. 2014). However, many spiders do, in fact, rely to a large extent on vision for their lifestyle.

Two families of spiders that are well known for their good vision are the Lycosidae (wolf spiders) and the Salticidae (jumping spiders) (Jackson and Pollard 2007). Almost all wolf spiders are cursorial hunters (Coddington and Levi 1991). Wolf spiders use visual cues to measure polarized light and distance estimation when homing (Ortega-Escobar and Ruiz 2014) and use elaborate visual displays while courting (Taylor et al. 2006). Wolf spiders have good image resolution, but poor colour

vision and cannot detect moving objects unless they are stationary themselves (Uetz and Roberts 2002). However, it is among jumping spiders that we find the most remarkable vision of all terrestrial arthropods.

Salticids are the largest family of spiders, with over 5000 species in more than 500 genera (Coddington and Levi 1991, Harland et al. 2012). They live in a wide variety of complex habitats with vastly different light conditions (Hu et al. 2012). Salticids use multiple sensory systems (Uetz and Roberts 2002), but the defining feature of salticids is their extraordinary vision (Harland and Jackson 2000). Salticids are one of the most highly visual groups of animals (Land 1969a). The behaviour of salticids, while being very complex, is also flexible (Jackson and Pollard 1996). It is their unique visual system which means salticids can have a wide range of visually-mediated behaviours, including navigation (Hoefler and Jakob 2006), aggressive behaviours (Jackson and Cooper 1991), courtship displays (Jackson 1983) and predatory behaviours (Jackson et al. 1990). All species of salticids are predators (Coddington and Levi 1991) that actively hunt and stalk their prey (Forster 1982), making them ideal candidates for research on vision. The behaviour of many different salticid species has been well studied (Hoefler and Jakob 2006), although possibly none as much as species in the genus *Portia*.

Portia are web-invading araneophagic salticids (Tarsitano et al. 2000) that have highly complex predatory behaviour. The preferred prey of *Portia* are web-building spiders, which are a very dangerous choice of prey, especially if they are large (Li and Jackson 1996). When hunting, *Portia* invade the webs of spiders but are occasionally injured, or even killed by the host spider (Jackson and Hallas 1986). Web building spiders generally have poor vision, and instead, effectively hunt by interpreting vibratory signals from their web (Coddington and Levi 1991). *Portia* hunt their prey using aggressive mimicry, a form of mimicry in which a predator deceives its prey (Jackson and Nelson 2011). When *Portia* invades a host spider's web, they mimic web signals to deceive the prey into coming out into the web. *Portia* have a variety of web signals they use when hunting; the signals *Portia* use depends on the host spider. For example, when the host spider is larger than *Portia*, it may be too risky to imitate the vibrations of a prey item caught in the web and so *Portia* will use a different signal to draw out the host spider (Tarsitano et al. 2000).

Salticids have a distributed visual system, with four pairs of simple camera-type eyes (Land 1999). One pair of 'primary' anterior median (AM) eyes is responsible for high spatial acuity and colour vision (Hu et al. 2012) and three pairs of secondary eyes, called the anterior lateral (AL), posterior median (PM), and posterior lateral (PL), are used for detecting movement (Zurek et al. 2010). Combined, the salticid visual system has an almost 360° field of view (Land 1985). Unlike vertebrate eyes, the four pairs of eyes are functionally specialised and have different visual tasks (Zurek et al. 2010). In general, bigger eyes have more acute vision, and only big animals are able to

have big eyes (Chittka and Spaethe 2007). However, salticids have managed to develop highly acute vision in very small eyes. This unique, distributed visual system separates the functions performed by the fovea and periphery of vertebrate eyes into the primary and secondary eyes, saving space, as characteristics such as spatial acuity, colour vision, and contrast sensitivity all compete within an eye (Zurek and Nelson 2012a). It is this 'division of labour' within the visual system which gives salticids such acute vision with such small eyes (Duelli 1978).

The primary eyes of salticids have the highest spatial acuity in relation to body size of any animal (Jackson and Pollard 1996, Zurek et al. 2015). The highest spatial acuity among salticids is that of *Portia*, with a spatial acuity of 0.04° (Heinze 2014). This is an order of magnitude better than the best spatial acuity found in an insect, the large dragonfly *Sympetrum striolatum*, which has a spatial acuity of 0.4°, yet these dragonflies are much bigger animals, with eyes larger than most salticids (Harland et al. 2012). The spatial acuity of salticid primary eyes exceeds that of many birds, and approaches that of primates (Jackson and Pollard 2007), with the human eye having a spatial acuity of 0.07° (Su et al. 2007).

In salticids, the primary eyes are responsible for object recognition, as well as mediating predatory and mating behaviours (Forster 1982). Behind the corneal lenses of the primary eyes is a long eye tube resembling a telescope (Blest et al. 1990). Small, boomerang-shaped retinae are located at the end of each of these eye tubes. Just in front of the retina, light passes through a second lens that magnifies the corneal lens, acting as a Galilean telescope (Williams and McIntyre 1980). It is this unique structure which allows the primary eyes to have such high spatial acuity, and is why most research into the salticid visual system has focused on the primary eyes (Zurek and Nelson 2012a). Additionally, the retinae of the primary eyes are tiered, with four tiers of photoreceptors (Williams and McIntyre 1980). These tiers act both as a focusing system (Land 1969a) and play a role in colour vision through chromatic aberration, where light from different parts of the spectrum come into focus at different distances behind the eye lens (Harland et al. 2012, Zurek et al. 2015). Colour is used as an important tool in species recognition (Land 1969a) and there are at least three types of photoreceptors in the primary eye cells with different spectral sensitivities (Koyanagi et al. 2008), including ultraviolet (Hu et al. 2012). Many salticids even visit flowers and forage on nectar (Jackson et al. 2001, Carvell et al. 2017), and ultraviolet is an important visual cue for flowers. The corneal lenses are a fixed part of the spider's exoskeleton (Land 1969a, b). However, six oculomotor muscles attached to the eye tubes allow a small amount of movement of the narrow retina, extending the field of view from c. 2°when stationary to about 60° (Land 1969b). Due to the narrow field of view of the primary retinae, the spider must move its retinae over the object in order to view it. The two primary retinae usually move in tandem but are also able to move independently of each other (Land 1969b). The range of motion of the primary retinae means that the spider can

shift it's 'gaze' towards objects of interest in the environment (Kaps and Schmid 1996). The centre of the retina (bend in the boomerang) has a higher density of photoreceptors than at the edges (Land 1969b) and it is thought that salticids mostly use this high acuity region of the retinae when scanning over an object of interest. The acute vision of salticids means they are able to identify objects at distances of up to 30 cm away (Tarsitano and Jackson 1994, Tedore and Johnsen 2015). High spatial acuity is vital for accurate object identification (Cross and Jackson 2014), one of the major roles of the primary eyes.

There is a large collection of literature which states that the main purpose of the secondary eyes is for motion detection (Land 1969a, Hill 1975, Duelli 1978, Forster 1979, Williams and McIntyre 1980, Blest 1983, Tarsitano and Jackson 1992, Tarsitano and Jackson 1994, Jackson and Pollard 1996, Tarsitano and Jackson 1997, Land 1999, Tarsitano and Andrew 1999, Harland and Jackson 2000, Jackson et al. 2006b, Zurek et al. 2010, Harland et al. 2012, Spano et al. 2012, Zurek and Nelson 2012a, Zurek and Nelson 2012b, Heinze 2014, Menda et al. 2014, Zurek et al. 2015, McGinley and Taylor 2016). The secondary eyes, in particular the PL eyes, are highly specialised motion detectors (Zurek et al. 2010). The retinal structure of all pairs of secondary eyes is a hexagonal lattice arrangement (Land 1969a). With a wide field of view and fixed retinae, the secondary eyes are perfectly suited for detecting movement in the visual scene (Land 1999), but this does not mean that motion detection is all the secondary eyes are capable of. Even though the spatial acuity of the secondary eyes is far lower than the spatial acuity of the primary eyes, it is equivalent to the acuity of visual insects, between 0.4°- 2° (Harland et al. 2012). While this may not be remarkable when compared to salticid primary eyes, many of these insects have impressive feature detection abilities (Harland et al. 2012). For example, dragonflies such as *Sympetrum striolatum*, with a spatial acuity of 0.4°, are sit-and-wait predators who hunt their prey using visually-guided interception methods during flight. Dragonflies are extremely effective predators, with up to a 97% success rate (Olberg et al. 2000). These predatory behaviours indicate that the insect's visual system is sufficient for highly proficient visually-mediated behaviours. Even though salticid secondary eyes are extremely good motion detectors, their spatial acuity shows that they could also be processing non-movement (spatial) information (Harland et al. 2012). Evidence of this has already begun to appear in the literature; Spano et al. (2012) found that the AL eyes were solely responsible for mediating the response to looming objects in front of the spider. Furthermore, information from the AL eyes alone is enough to elicit predatory behaviours in response to a prey item (Zurek et al. 2010). If the secondary eyes are processing more than just movement information, and in particular are processing some spatially-based information, then, when the spider turns to face the object with the primary eyes, the retinae may have faster and more targeted scanning patterns.

Body size is the best predictor for brain size in an animal (Chittka and Niven 2009). For instance, whales can have brains weighing up to 9 kg and a human brain weights between 1.25 and 1.45 kg (Chittka and Niven 2009), yet the brain of a salticid is only the size of a poppy seed (Jackson and Harland 2009, Menda et al. 2014). Small nervous systems have fewer neurons (Niven and Farris 2012), which may lead people to believe that smaller animals are behaviourally limited by their nervous system. However, despite having small nervous systems, many invertebrates show highly complex and flexible behaviours (Giurfa 2015). Take bees, for example: they are very small, with small nervous systems, yet they possess an impressive ability to learn and memorize tasks (Zhang et al. 2005). Recently, a study by Loukola et al. (2017) investigated the behavioural flexibility of bumblebees. Bees were given the task to transport a small ball to a specific location, after which they were given a reward. Bees learnt more efficiently when observing a live or model demonstrator complete the task, compared to a "ghost" demonstration or no demonstration at all (Loukola et al. 2017). This shows the impressive cognitive and behavioural flexibility of bees, and their ability to solve novel problems not encountered in nature through social learning (Loukola et al. 2017). Bees are not the only small animals to possess impressive cognitive abilities; many insects have remarkable cognitive abilities and extensive social structures supported by minute nervous systems (Chittka and Niven 2009, Giurfa 2015).

Salticid behaviour is often described as more mammal-like than invertebrate-like (Harland and Jackson 2000). Salticids have large brains in relation to their body size, but the absolute size of their brain is still miniscule compared to the brains of mammals (Harland and Jackson 2000). Unlike computers, neurons cannot be shrunk, so the small brain size of a salticid means it has fewer neurons (Niven and Farris 2012). Having fewer neurons should reduce the sensitivity of sensory systems and the accuracy of motor systems (Niven and Farris 2012). Yet, salticids have shown impressive cognitive abilities. Tarsitano and Jackson (1997) showed that *Portia fimbriata* was able to make complex detours in order to reach a lure (dead prey spider). The spiders were able to complete these detours even when the correct route meant initially moving away from the lure, as well as when it meant losing sight of the lure. These detours are on par with detours made by vertebrates (Tarsitano and Jackson 1997), and demonstrate the cognitive abilities used by these spiders. Detouring is a cognitively challenging task, as the animal must maintain a representation of the goal while losing sight of the goal (Tarsitano 2006) The ability of salticids to plan and problem solve, including their ability to complete complex detours, is impressive considering the size of their nervous system (Cross et al. 2007). Limited neural capacity is often thought to create strong behavioural limitations, yet salticids have managed to overcome many neural limitations associated with their small brains. This is in part due to their highly acute, unique, distributed visual system (Menda et al. 2014).

Priming refers to a wide range of behavioural phenomena (Meeter and Van der Stigchel 2013) and the effect of priming on many different sensory systems (i.e. visual, olfactory) can influence an animal's behaviour. Priming is where exposure to one stimulus (i.e. perceptual pattern) influences the response to another stimulus. In humans, the effects of priming have been well studied, in particular within the visual system (Árni and Campana 2010). A person's gaze is almost always automatically drawn to objects of importance, especially if they have encountered those objects before (Árni and Campana 2010). Priming affects attentional mechanisms (Blough 1989); with the effects of priming increasing with repeated exposure to the object, improving both accuracy and reaction times (Wiggs and Martin 1998). The effects of priming are often rapid (Meeter and Van der Stigchel 2013), but we do not have control over the memory systems involved in priming (Árni and Campana 2010). Therefore, both relevant and irrelevant objects can be involved in priming; resulting in either positive or negative effects on the response (Huang et al. 2004). Unlike memory, priming in humans does not tend to improve with age, remaining relatively stable from the ages of 3 to 80 (Wiggs and Martin 1998). Even when the search task is easy, priming can have a strong effect on the response of the individual (Árni and Campana 2010). While the effects of priming have been well documented in humans (Blough 1989, Árni and Campana 2010), there has been far less research into the effects of priming in non-human animals.

Most research into priming of non-human animals has focused on vertebrates, including mice (Bronson 1979, Hurst 1993), monkeys (McPeek and Keller 2001), zebrafish (Cruz and Oliveira 2015), and blue jays (Bond and Kamil 1999, Goto et al. 2014). Early research into priming in nonhuman animals looked at the effects of pheromones on the behaviour of mice, where, for example, the presence of male pheromones accelerates female ovulation (Bronson 1979). In non-human animals, visual priming is often compared to search images, where repeated exposure to a food source allows the animal to detect that food source more efficiently (Blough 1989, 1991). In other words, previous exposure to a food type 'primes' the animal's visual system to be able to identify that food more easily than others. For example, Bond and Kamil (1999) found that blue jays were less able to detect moths during a visual search as they became more cryptic against the background. However, both response time and accuracy improved with priming and the effects of priming were greater as the background became more cryptic (Bond and Kamil 1999). Priming creates a search image, improving the foraging abilities of the blue jays when looking for the cryptic moths. Stronger priming effects with cryptic prey have been reported in various species (Bond and Kamil 1999, Cross and Jackson 2009, Cross and Jackson 2010).

Visual systems have to deal with complex environmental scenes (Fremouw et al. 1998). When predators search for cryptic prey they use a wide range of cognitive abilities, as predators must be able to discriminate prey from complex natural backgrounds (Bond and Kamil 1999).

Attention can be drawn to particular objects within the environment through different cognitive processes, including associative cuing and priming (Goto et al. 2014). Although visual priming in nonhuman animals has been most extensively studied in birds, such as pigeons (Blough 1989, 1991, 1992, Gibson et al. 2015), barn owls (Hazan et al. 2015), and blue jays (Bond and Kamil 1999, Goto et al. 2014), there has been some research into priming among invertebrates.

Recently, there have been a few studies of priming in salticids (Cross et al. 2007, Cross and Jackson 2010, Carvell et al. 2017). These studies have focussed on cross-modality priming, in which priming of one sensory system influences the response of another. Cross and Jackson (2009) investigated how vision and olfaction interacted in *Evarcha culicivora. E. culicivora* is an East African salticid which preferentially feeds on blood-fed mosquitos. When primed with the odour of their preferred blood-fed mosquito prey, spiders were better able to find the prey, especially when the prey were set against a cryptic background (Cross and Jackson 2009). Cross and Jackson's (2009) study shows that priming can influence salticid behaviour, yet there have been no studies into visual priming within the distributed salticid visual system, specifically, priming by the secondary eyes to the primary eyes. This is especially relevant because salticid behaviour is characterised by visual detection of motion by the secondary eyes which triggers and optomotor response whereby the animal, having detected motion in the periphery, swivels around to inspect the source of motion closely with its high-acuity primary eyes. This behaviour suggests that perhaps some level of filtering by the secondary eyes may occur: some targets detected by the secondary eyes may not be 'deemed' worthy of closer inspection, or indeed, basic shape processing by the secondary eyes may 'prime' the primary eyes as to what type of shape to scan for.

Almost all animals with good vision have eye movements (Land 1999). Eye movements are historically important for understanding cognitive processes in many animals, most commonly in humans (Hayhoe and Ballard 2005, Friedrich et al. 2016). Tracking eye movements is an objective method to help understand the strategy of information gathering (Brychtova and Popelka 2012). Eye-tracking is used to understand information gathering techniques for both reading and image processing; these techniques are used frequently in driving, marketing, and air traffic management research (Friedrich et al. 2016). For example, humans direct their attention to objects of importance with eye movements (Brascamp et al. 2011) and are excellent at quickly extracting information from a visual scene (Kirchner and Thorpe 2006).

The ability of an animal to quickly and accurately direct its attention to objects of interest within its environment is an important aspect of survival for many species (McPeek and Keller 2001, Gibson et al. 2015). The information-gathering processes used are likely to differ significantly between animals due to the different cognitive processes and visual systems involved. Now, similar research is being done on the pattern of eye movements to infer the cognitive processes (Hirata et

al. 2010, Hazan et al. 2015) of other animals, such as chimpanzees (Hirata et al. 2010), rabbits (Collewijn 1977), and birds, including barn owls (Hazan et al. 2015), chickens (Pratt 1982), and peacocks (Yorzinski et al. 2013, Yorzinski et al. 2015).

Mike Land (1969b) developed a specialised opthalmoscope for looking into the salticid retina, and was the first person to investigate the retinal movements of a salticid. Using the opthalmoscope, Land (1969b) described four patterns of movement of the primary retinae: spontaneous movement, saccades, tracking, and scanning. When the spider turns to view an object with its primary eyes, saccades are used to quickly bring the object into the field of view of the retina, the retina may then switch to scanning (Land 1969b). These eye movements allow salticids to scan interesting parts of their environment (Land 1969a) and are critical for understanding the salticid visual system (Harland et al. 2012).

For this research, I am investigating the effects of visual priming on the salticid visual system. For this, I use a specially-designed eye-tracker, based on Land's (1969a) original opthalmoscope. Here, a salticid opthalmoscope is coupled with an infrared video that can record retinal movements to a known object which is presented to the salticid. The object is projected from a computer to a specialised screen. Salticids willingly respond to virtual stimuli (Harland and Jackson 2002, McGinley and Taylor 2016), which makes them an ideal animal to use with an eye-tracker. My research will focus on how visual priming of the secondary eyes with non-moving shapes influences the saccadic and scanning patterns of the primary retinae, as measured using the eye-tracker. Studying visual priming between the secondary and primary eyes will give us some understanding as to how the different eyes interact within the visual system. Additionally, understanding how information is gathered within the visual system can give us insight into the cognitive processes involved (Friedrich et al. 2016).

This research focuses on visual priming in the distributed visual system of a salticid. This thesis consists of only three chapters, with chapter one being the introduction. Chapter two is the only data chapter in the thesis and is written in the style of publication. In this chapter visual priming is tested using a specially-designed eye-tracker to record eye movements of a salticid. This thesis has only a single data chapter as the experiment and subsequent data analysis was extremely time intensive. There has been no previous research into visual priming in salticids and as a result, there was no straight-forward method of data analysis. The third and final chapter is the discussion and conclusion chapter. Repetition has been avoided when possible but due to the nature of this thesis there are significant amounts of repetition, especially in the introduction of the second chapter.

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Chapter 2:
The effects of visual priming on retinal scanning patterns

Marpissa marina set up in front of the eye tracker (Photo: L. Scott)

Introduction

Spiders are one of the most diverse group of organisms on earth (Coddington and Levi 1991). Within spiders, jumping spiders (Salticidae) are the largest family, with over 5000 species in more than 500 genera (Jackson and Pollard 1996, Cross and Jackson 2017). Salticids live in complex habitats and are found on every continent except Antarctica (Jackson and Hallas 1986, Li and Jackson 1996). Salticids are a highly specialised family of spiders (Coddington and Levi 1991), with extremely complex behaviours mediated by their visual system (Land 1969a, Forster 1982). Salticids actively hunt and stalk their prey, as opposed to catching prey using a web, as many other families of spiders do (Forster 1979, Harland and Jackson 2000a). Being active predators, salticids benefit from having highly developed vision, by gaining accurate information about the identity, size, location, and behaviour of their prey (Harland and Jackson 2002). Vision is not only important for hunting, but is also vital in mediating other complex behaviours, including interspecific interactions (Jackson 1983, Tedore and Johnsen 2015). Having to detect, identify, and locate both prey and mates, salticids face many cognitively similar tasks as larger vertebrate predators (Forster 1982). However, being invertebrates, they must complete these tasks with only a small nervous system.

Even though the brains of salticids are smaller in absolute terms than the brains of larger species, their brains are larger in proportion to their body size (Eberhard 2011). There are strong limitations as to how much information can be retained in a brain at one time, especially in animals with small brains (Cowan 2010, Goto et al. 2014). Even with a small nervous system, salticids have the capacity for working memory (Cross and Jackson 2014), problem solving, (Jackson and Nelson 2011), planning (Tarsitano and Jackson 1994), and numeracy (Nelson and Jackson 2012, Carvell et al. 2017). This shows, along with the cognitive abilities of other invertebrates, that relatively small amounts of nervous tissue can be enough to perform complex behavioural tasks (Eberhard 2011). Within the salticid nervous system, the most distinctive aspect is the large size of the optic nerves, with these being almost as large as the eyes themselves (Hill 1975). This gives an indication as to how vital visual information is for controlling behaviour in salticids.

Salticids are some of the most highly visual animals on the planet (Land 1969a), due to their unique, distributed visual system. The salticid visual system contains four pairs of functionally distinct eyes; one large pair of forward facing (primary) anterior median eyes, and three pairs of smaller secondary eyes (anterior lateral, posterior median, posterior lateral) (Harland and Jackson 2002). Each eye sends its information to the brain via its own optic nerve (Hill 1975). Indeed, it is the separation of the visual system that enables salticids to have the most acute vision for their size of

any animal (found in *Portia* with an acuity of 0.04°), even exceeding the spatial acuity of many vertebrates (Harland et al. 2012, Heinze 2014).

Most of the research into the salticid visual system has focused on the primary eyes (Zurek and Nelson 2012a). The primary eyes are functionally distinct from the secondary eyes and control most of the complex visually-mediated behaviours that for which salticids are famous (Su et al. 2007). The primary eyes are responsible for high spatial acuity and colour vision (Williams and McIntyre 1980, Harland and Jackson 2000b). The boomerang-shaped retinae of the primary eyes are located at the end of long eye tubes which extends back into the spider's head, and a small lens placed in front of the retina creates a Galilean telescope-like structure (Blest et al. 1990, Harland et al. 2012). Without movement, the primary eyes have a very narrow field of view, but muscles attached to the eye tubes enable each retina to move independently, extending the field of view of the primary eyes about 30° to either side of the vertical mid-plane (Tarsitano and Jackson 1992, McGinley and Taylor 2016). The structure and high acuity of the primary eyes makes them ideal for detecting detail in objects in the environment. In mediating a repertoire of visual behaviours (Tarsitano and Jackson 1997, Jackson et al. 2006a), the primary eyes are incredibly important in controlling salticid behaviour and if they are covered, most behaviours also cease (Land 1969b).

The secondary eyes are exceptional motion detectors (Land 1999) but have lower spatial acuity than the primary eyes (Land 1969a). When movement is detected in the field of view of the secondary eyes, the spider turns to face the object with the primary eyes (Duelli 1978, Blest 1983, Jackson and Hallas 1986, Tarsitano and Jackson 1994, Zurek et al. 2010); this turning behaviour is maintained even when the primary eyes are covered (Forster 1979). Combined, all three pairs of the secondary eyes give salticids a nearly 360° field of view (Zurek and Nelson 2012b). While the role of the secondary eyes has largely been considered as motion detection, there has been some evidence to indicate that they control more aspects of salticid behaviour (Spano et al. 2012). Eyes need reasonable acuity to be able to accurately detect movement (Zurek and Nelson 2012b) and the secondary eyes have a higher spatial acuity than has been previously thought (Spano et al. 2012). While the secondary eyes do not have the same acuity as the primary eyes, their acuity is similar to that of the most highly-visual insects (Harland et al. 2012), suggesting potential feature-detection abilities, and a possible role in mediating more than just movement detection behaviour.

In his seminal work on salticid vision, Mike Land (1969a) described four patterns of movement of the primary retina; spontaneous movements, saccades, scanning, and tracking. Scanning is unique to salticids (Jackson and Harland 2009) and the patterns of scanning are complex, but mostly predictable, as the same stimulus will generally induce a similar scanning response (Land 1969b). Because the eye movements of the primary eyes allow salticids to inspect interesting parts

of their environment (Heinze 2014), understanding their pattern of movements is a crucial aspect of understanding the salticid visual system (Harland et al. 2012).

Exposure to a stimulus can influence the response to another stimulus; this is referred to as priming. Priming can influence a single, or multiple sensory systems. When multiple sensory systems are involved in the priming process, this is called cross-modality priming. Previous studies into priming in salticids have solely looked into cross-modality priming, involving the olfactory and visual sensory systems, and in terms of behavioural decision-making (Cross and Jackson 2009, Carvell et al. 2017). These priming studies have shown that priming can have a marked effect on salticid behaviour. However, no research has exclusively considered visual priming within the distributed visual system of salticids. Here, I was interested in the saccadic and scanning patterns of the primary eyes in response to visual priming of the secondary eyes.

The salticid species used here was *Marpissa marina*, an endemic New Zealand species whose primary habitat is the spray zone of stony beaches (Jackson et al. 2006b). New Zealand has a depauperate salticid fauna, with no other species sharing its habitat with *M. marina* (Jackson et al. 1990). Like most salticids, *M. marina* is a cursorial insect hunter (Jackson et al. 2006a), actively hunting and stalking their prey by sight (Jackson et al. 1990, Jackson et al. 2006b). Vision also plays a large role in the intraspecific interactions of *M. marina* (Jackson et al. 1990). Salticids have highly-developed aggressive interactions; in *M. marina* males are able to perceive size differences in other males at a distance, which is important for quickly settling conflicts (Jackson and Cooper 1991). Male *M. marina* are also known to have elaborate visual courtship display behaviours towards females, which vary depending on the female and her location (Jackson et al. 1990).

My aim was to determine whether priming of the secondary eyes of *M. marina* influences the scanning response of the primary eyes. This was done by initially presenting the posterior lateral (PL) eyes with a non-moving shape stimulus, and then presenting the primary eye with a non-moving shape stimulus and recording the scanning pattern of the primary retinae with a specially-designed salticid eye-tracker. I used both expectation-confirmation (the same stimulus presented to the secondary followed by the primary eyes) and expectation-violation (different stimuli presented to the secondary followed by the primary eyes) priming experiments. I predicted that, due to priming, the primary retinae would, at least when first presented with a stimulus, use a scanning pattern in accordance with the object previously presented to the PL eye.

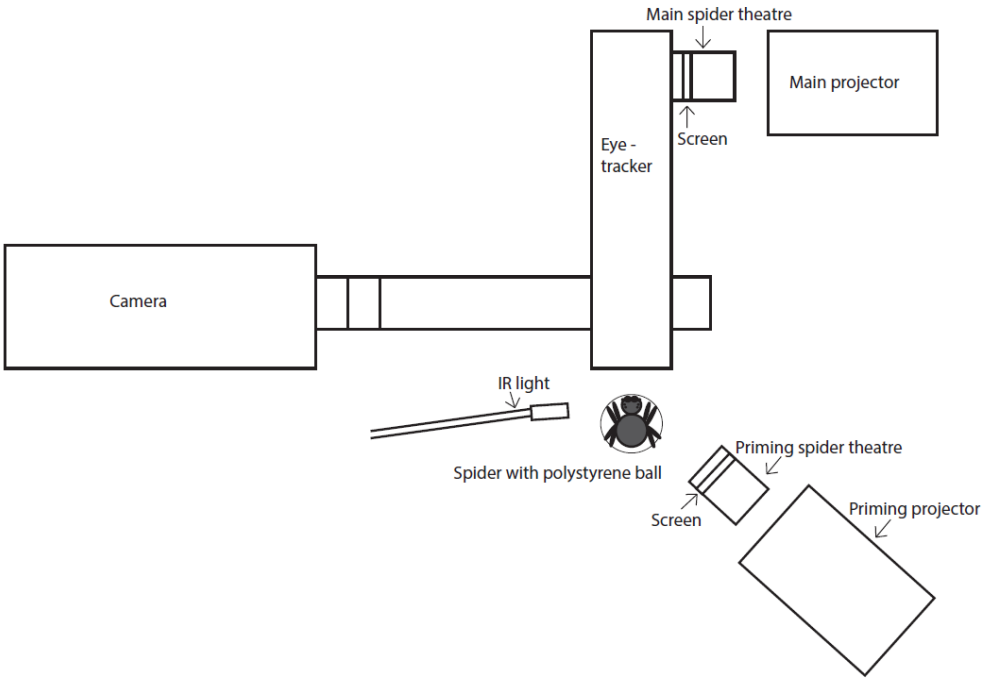
Methods

Eleven adult female *Marpissa marina* were used for this experiment. Only adult female spiders were used in this experiment, as female spiders are often more responsive and willing to

complete tasks in behavioural studies than males (Zurek et al. 2010). Female *M. marina* have a robust, grey-black abdomen and cephalothorax, black legs and a band of white hairs on the clypeus (Jackson et al. 2006b). The spiders used for this experiment were collected from Birdling's flat, 47 km south of Christchurch in October 2016. All spiders were held in a temperature and light-controlled laboratory set to 24°C - 26°C, with a photoperiod of 12L:12D (lights on at 07:00). Each spider was housed separately in enriched clear plastic 1 L jars as described by Zurek et al. (2010). Spiders were fed one housefly (*Musca domestica*) weekly. To keep hunger levels consistent throughout testing, each spider was tested five days after being fed. All experiments were carried out during the hours of 09:00 and 15:00.

For this experiment, the retinal movements of the primary eyes were recorded using a specially-designed eye-tracker; designed to record salticid retinal movement while simultaneously displaying digital stimuli (Figure 1). Stimuli were back-projected onto a white screen through a lens placed 10 mm from a projector (AAXA M2 micro projector), with the screen and lens being held in place using a 3D printed 'spider theatre' attached to the eye-tracker. Spiders were held in place in front of the eye-tracker using a dental micro-applicator dabbed in bees' wax, which was attached to the spiders' cephalothorax. Using a micromanipulator, the spider was carefully positioned in front of the eye tracker, so that the primary retinae were in full view. The primary retinae of the salticid was then illuminated using an infrared light shone directly through the spiders' cephalothorax. Spiders were given a small 10 mm polystyrene ball to freely walk on but which prevented the movement of their cephalothorax. A drop cup was placed underneath the spider, so that if they tried to jump (and therefore dropped the ball) the ball was caught and stayed close enough to the spider that they were able to pull the ball back up using their drag-line. While the polystyrene balls are heavier than the spider, they are light enough for the spiders to easily walk on for extended periods of time (Zurek et al. 2010). A pre-determined stimulus was then able to be projected to the spider through the eye tracker, and the response of the primary retina was recorded through an infrared camera for further analysis. The stimuli presented to the spiders were simple black and white images created in Adobe Photoshop CS6. The two stimuli used were a horizontal bar and a circle. In this experiment, a second projector was set up alongside the eye-tracker to project a stimulus to the left primary lateral eyes (LPL). Due to space constraints, only the LPL eye was able to be primed.

(A)



(B)

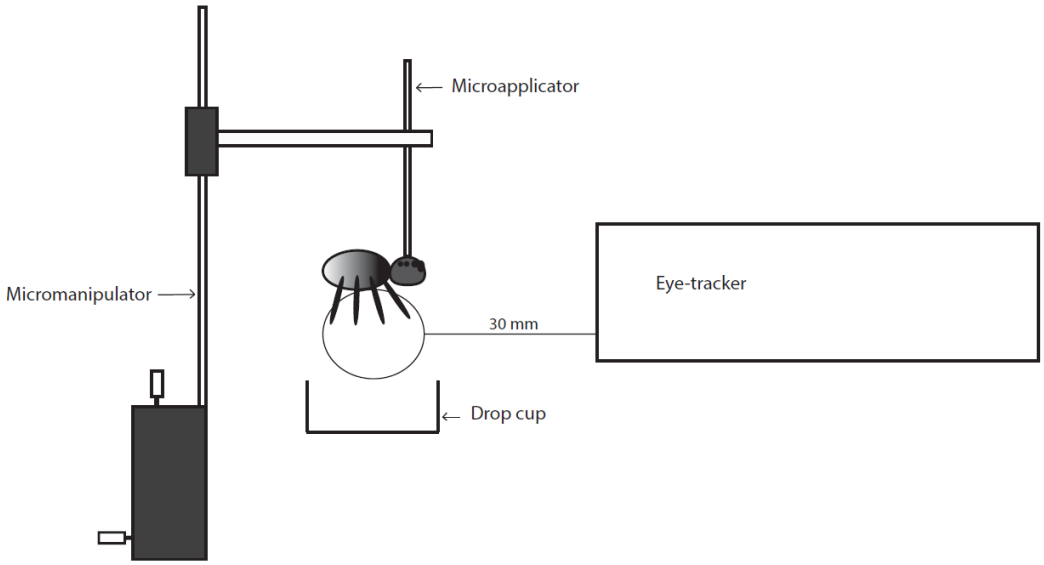


Figure 1. Experimental set up for the visual priming experiments with *Marpissa marina*. (A) Aerial view of the eye tracker and projectors. (B) Side-view of spider in front of the eye-tracker. Priming projector and spider theatre project priming stimulus onto the LPL eye. Main projector and theatre project main stimulus to the primary eyes through the eye-tracker. Response of the primary retinae are recorded using an IR camera attached to the eye tracker. During the experiments a spider is attached to a dental microapplicator and held in place using a micromanipulator.

I used six priming paradigms, and all test spiders were each tested on all paradigms. Each paradigm consisted of a priming stimulus of either a bar or a circle, which was presented to the LPL eye, followed by the main stimulus of either the same (matched) or alternative (mismatched) stimulus presented to the primary eyes (Figure 2). The bar and circle stimuli were chosen as they are

both very simple stimuli but elicit very different search patterns from the spider. In each test, the priming stimulus was presented to the LPL eyes for 500 ms and then for the 'immediate' paradigms, the main stimulus, presented to the primary eyes, followed immediately after. In the case of the 'delayed' paradigms, there was a 500 ms inter-stimulus interval between the priming and the main stimulus. The main stimulus was presented to the primary eyes for one minute, after which there was a two-minute break (inter-session interval) and then the entire priming test was repeated. Therefore, in total, there were two iterations for each test.

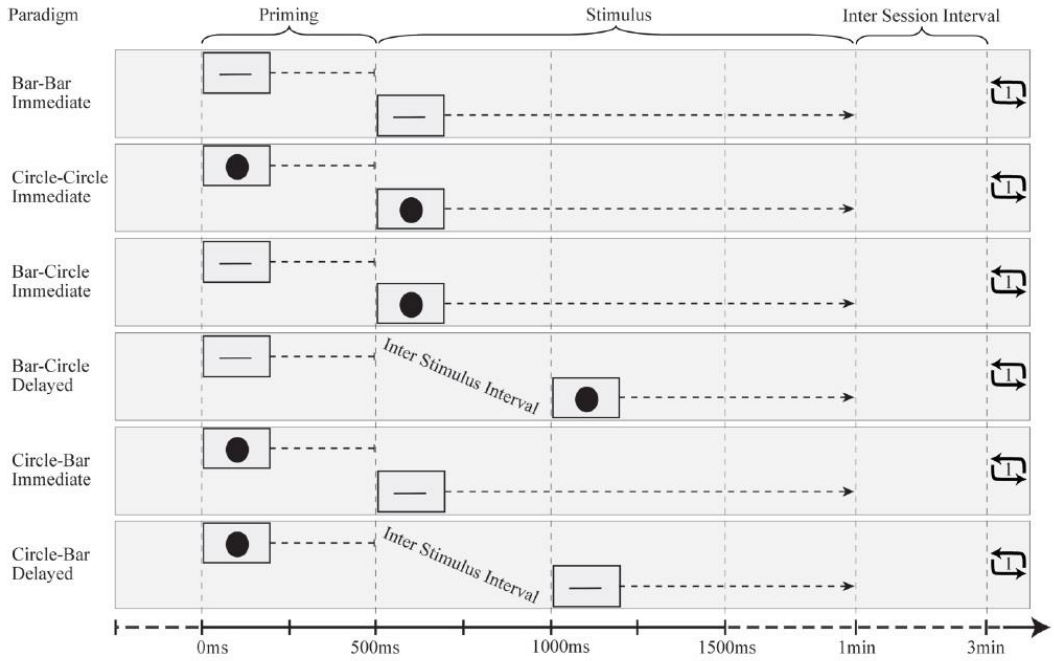


Figure 2. The six different priming paradigms used in this study with both the bar and circle stimulus. The priming stimulus was always presented to the LPL eyes for 500 ms. The main stimulus was then presented to the primary eyes either immediately or after a 500 ms inter-stimulus delay. Each paradigm was presented to the spider twice, the second iteration after a 2-minute interval. For all paradigms, n=11.

During a testing session, each spider was tested on all six paradigms. Between each of the tests, there was a 15 min break in which all the projectors and lights were turned off and the spider sat in darkness. This allowed the spider to rest and reduced any learning effects between paradigms. If any of the tests failed, i.e. the retinae did not saccade in response to the priming stimulus, or the retinae did not initially scan the main stimulus, then the failed tests were tested again one week later. Without a clear saccade (or scanning motion) it was impossible to know whether the priming stimulus was perceived by the spider. This was repeated until all the spiders had responded to all six of the priming paradigms, which sometimes took several months.

Prior to the priming experiments starting, a calibration video was presented to the primary eyes. This calibration video consisted of a small, black dot which flashed at three points on the

screen, in the shape of a right-angle triangle. The calibration video served two main purposes: firstly, once the spider's retinae focused on the three points, it meant we were able to account for slight variations in the position of the spider once it was set up, as well as the position of the stimulus on the screen. This enabled me to normalize these variations across videos for data analysis. Secondly, the calibration video gave an indication to the responsiveness of the spider. The calibration stimuli often elicited an immediate and clear response from the spiders, yet if a spider did not respond it was a good indication it would not respond to the priming tests. If a spider did not respond to the calibration video, the testing session was immediately stopped, and the spider was tested on another day.

Videos were tracked using the MTrackJ function in ImageJ. Tracking started three seconds before the priming stimulus was shown and finished once the retina had stopped scanning the stimulus, moved off the screen, or after 15 s. Videos were captured at 30 fps and for each frame the centre of the boomerang-shaped retina was tracked. Both left and right retina were tracked (see Appendix 1), but for simplicity only the track of the left retina was used in the analysis. We can infer the results from the left retina will also apply to the right retina, as movement is almost always mirrored between the two eyes (Land 1969b).

For this analysis I was only interested in scanning motions; therefore periods of no retinal movement were removed from the tracks using MATLAB. Here, periods of no retinal movement were identified as five or more continuous points where the coordinates stayed the same. The identical points were then removed from the dataset prior to analysis. The remaining tracks were then split into three sections for the immediate priming paradigms and four in the case of the delayed priming paradigms: spontaneous retinal activity prior to priming (depicted in yellow in the figures; for full set see Appendix 2), during priming (red), during the inter-stimulus interval (for delayed paradigms only; purple), and during the presentation of the main stimulus (gradient from blue to green; indicating the scanning pattern over time).

The number of active tracks (points in which the retina moved) was calculated for each track. I used paired t-tests to compare the mean activity levels between the priming paradigms. T-tests were performed between the two matched paradigms, as well as between the matched and mismatched paradigms, where the main stimulus was the same (bar-bar versus circle-bar etc.). Finally, I used t-tests to compare activity between the immediate and delayed mismatched paradigms, where the main stimulus was the same.

Additionally, the distance from each point to the edge of the main stimulus was calculated for each track. These distance measures were then plotted against time and were analysed using a generalised additive mixed effect model (GAMM) to identify the trends in the data and see how

targeted the tracks were with respect to the edge of the stimulus. The modelled tracks were then compared between the first and second iteration for each priming paradigm. The modelled tracks for both iteration 1 and 2 were then compared between the matched and mismatched paradigms for the main bar stimulus (bar-bar compared to both circle-bar and circle-bar delay), as well as the main circle stimulus (circle-circle compared to both bar-circle and bar-circle delay). The immediate and delayed paradigms were also compared (bar-circle and bar-circle delay; circle-bar and circle-bar delay).

Lastly, the second iteration tracks for each priming paradigm were combined and the combined tracks were used to create scanning heatmaps for each paradigm (equivalent to gaze heat maps when studying mammals). Heatmaps were created using the second iteration tracks, to show the clearest changes in scanning patterns across the matched and mismatched paradigms. This provides an indication of what aspects of a stimulus elicit strong scanning behaviour.

Results

Overall, visual inspection of the individually-plotted tracks indicated a clear effect of priming in some (but not all) tests. However, the effect of priming on the scanning patterns varied largely between spiders and across tests. All plots are compiled together in Appendix 2 and are grouped by priming paradigm and ordered by clarity of priming effect. When it was clear, for example as depicted in Figure 3, when a spider had been primed with a circle but the primary eyes were presented with a bar, the scanning pattern, especially in the second iteration, clearly showed circular scanning patterns of the priming stimulus and not the typical horizontal pattern of movement of the main bar stimulus (Figure 4).

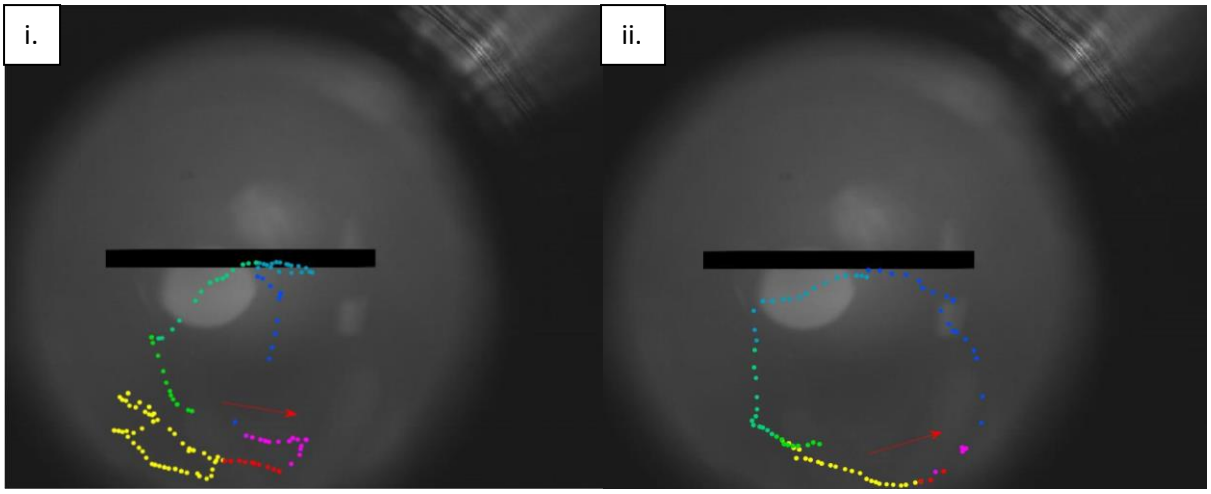
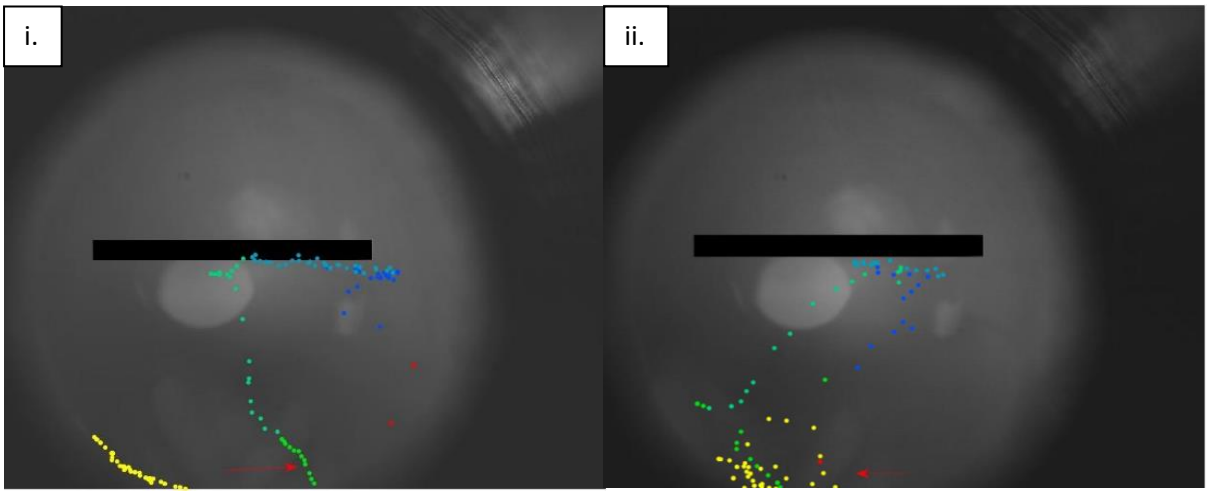


Figure 3. Example of a clear priming effect in the circle-bar delay priming paradigm. Yellow: Spontaneous activity before presentation of any stimuli. Red: During priming stimulus. Red arrow indicates the initial direction of saccade. Purple: Inter-stimulus delay. Blue to Green: During presentation of the main stimulus. i. Iteration 1. ii. Iteration 2.

(A)



(B)

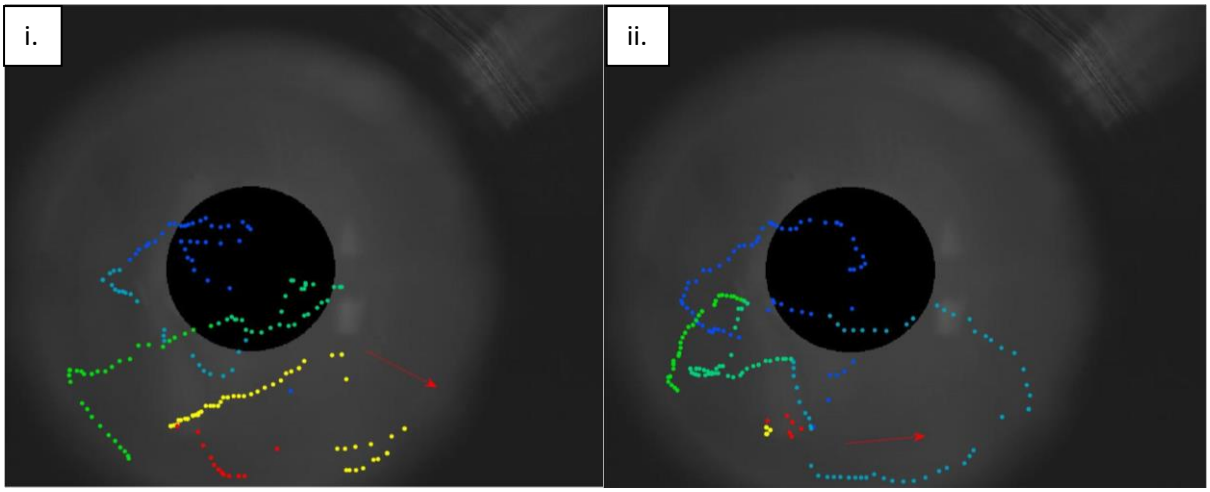


Figure 4. Examples of typical scanning patterns for each stimulus. (A) Example of horizontal scanning patterns for the bar stimulus. (B) Example of the circular scanning patterns for the circle stimulus. Yellow: Spontaneous activity before presentation of any stimuli. Red: During priming stimulus. Red arrow indicated the initial direction of saccade. Blue to Green: During presentation of the main stimulus. i. Iteration 1. ii. Iteration 2.

Results of the paired t-tests indicate that there was a significantly different response towards the two stimuli (Table 1). In the matched paradigms, tracks were significantly more active in the bar-bar paradigm compared to the circle-circle paradigm. Priming of the bar stimulus significantly increased the activity of the retinal tracks; with both the bar-circle, and the bar-circle delay paradigms being more active compared to the circle-circle paradigm. There was no significant difference in track activity between bar-circle and bar-circle delay paradigms. Priming of the circle stimulus did not influence retinal activity in both the circle-bar, and the circle-bar delay paradigms

when compared to the bar-bar paradigm. There was, however, a significant increase in activity in the circle-bar delay paradigm, when compared to the immediate, circle-bar.

Table 1. Paired t-tests comparing the mean activity of the retinal tracks between the matched and unmatched paradigms, and between the immediate and delayed paradigms. Significant p-values are marked with an asterisk.

Paradigm	Test statistic	df	P value
Bar-bar: Circle-Circle	3.1114	21	0.005*
Bar-bar: Circle-Bar	1.9224	21	0.069
Bar-Bar: Circle-Bar Delay	0.2477	21	0.807
Circle-Circle: Bar-Circle	-2.1539	21	0.043*
Circle-Circle: Bar-Circle Delay	-3.2218	21	0.004*
Bar-Circle: Bar-Circle Delay	-0.9521	21	0.352
Circle-Bar: Circle-Bar Delay	-2.1214	21	0.046*

When measuring the distance from each point in the track to the edge of the stimulus (Figure 5), there was no significant difference between iterations in the variation of the distance of the tracks to the edge of the stimulus for any priming paradigm, except circle-bar, which was significant ($F= 4.022$, $p=0.045$). While the variation between iterations for the circle-circle paradigm was not significant, there was a much lower level of variation (in the first iteration track) than in all other priming paradigms.

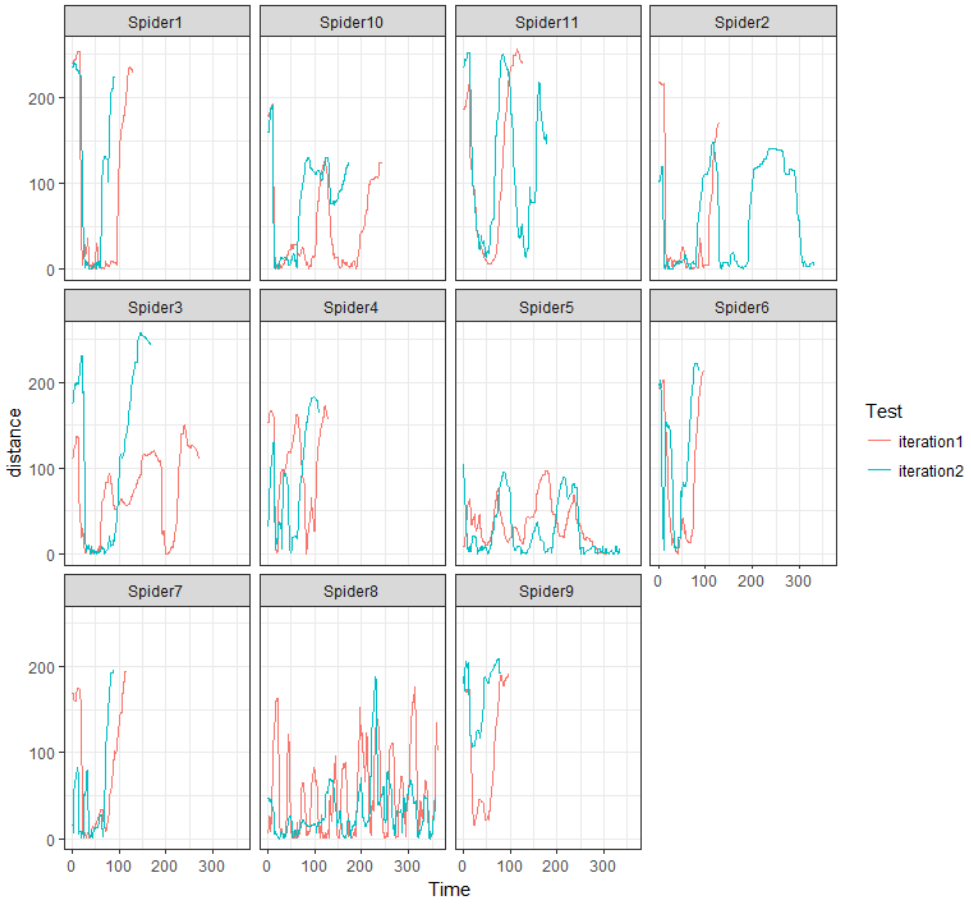
When comparing the distance measures between paradigms, I found a significant difference between both delayed mismatched paradigms and the matched paradigms (Table 2). There was significant variation between the first iteration of both bar-bar and circle-bar delay and between the first iterations of circle-circle and bar-circle delay. Interestingly, I also found a significant difference in variation between the circle-bar and circle-bar delay paradigms (Table 2). There was no significant difference between the distance measures between bar-bar and circle-bar; circle-circle and bar-circle; or bar-circle and bar-circle delay. Generally, it was interesting to note how similar the pattern of scanning behaviour was between iterations, with individuals differing between each other, but being consistent within subject (Figure 5).

Table 2. Results of the GAMM analysis between the first iterations of the matched and mismatched paradigms, and the immediate and delayed paradigms. Significant p-values are marked with an asterisk.

Paradigm	Estimated df	F statistic	P value
Bar-Bar: Circle-Bar	1.00	1.765	0.184
Bar-Bar: Circle-Bar Delay	13.84	4.604	<0.001 *
Circle-Bar: Circle-Bar Delay	16.41	6.942	<0.001 *
Circle-Circle: Bar-Circle	1.00	0.000	0.983
Circle-Circle: Bar-Circle Delay	6.22	4.631	<0.001 *
Bar-Circle: Bar-Circle Delay	1.00	1.301	0.254

Results of the scanning heatmaps show a significant change in the general scanning pattern between the matched and mismatched paradigms (Figure 6). This trend is most clearly seen between the bar-bar and the circle-bar delay. The bar-bar heatmap shows a strong trend towards scanning the main bar stimulus; whereas the circle-bar delay heatmap shows strong circular scanning patterns, with almost no tracking of the main bar stimulus. Both immediate mismatched paradigms show a less targeted scanning pattern towards the main stimulus, indicating an effect of priming. However, in the case of the circle-bar and circle-bar delayed paradigms, the delayed heatmap shows a more targeted pattern of scanning towards the primed stimulus than the immediate heatmap. Interestingly, the bar-circle paradigm shows more horizontal scanning patterns, typical of the bar stimulus, than the delayed paradigm.

(A) i.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distance
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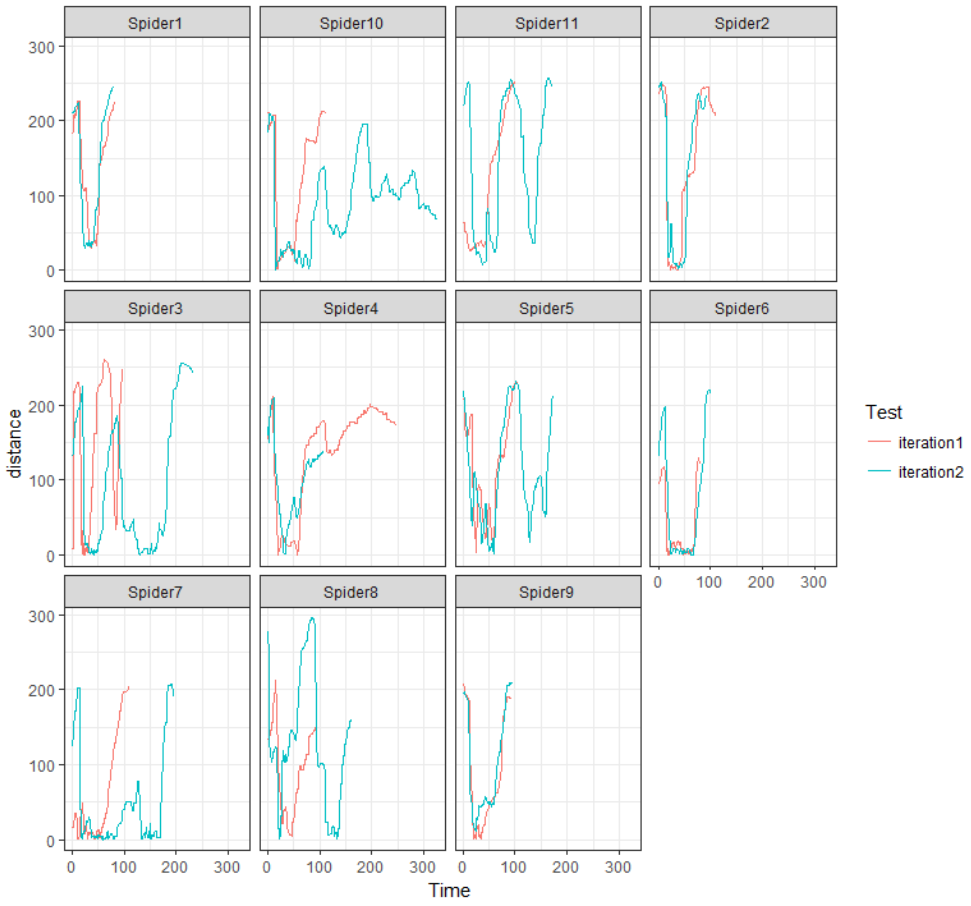
iteration2

ii.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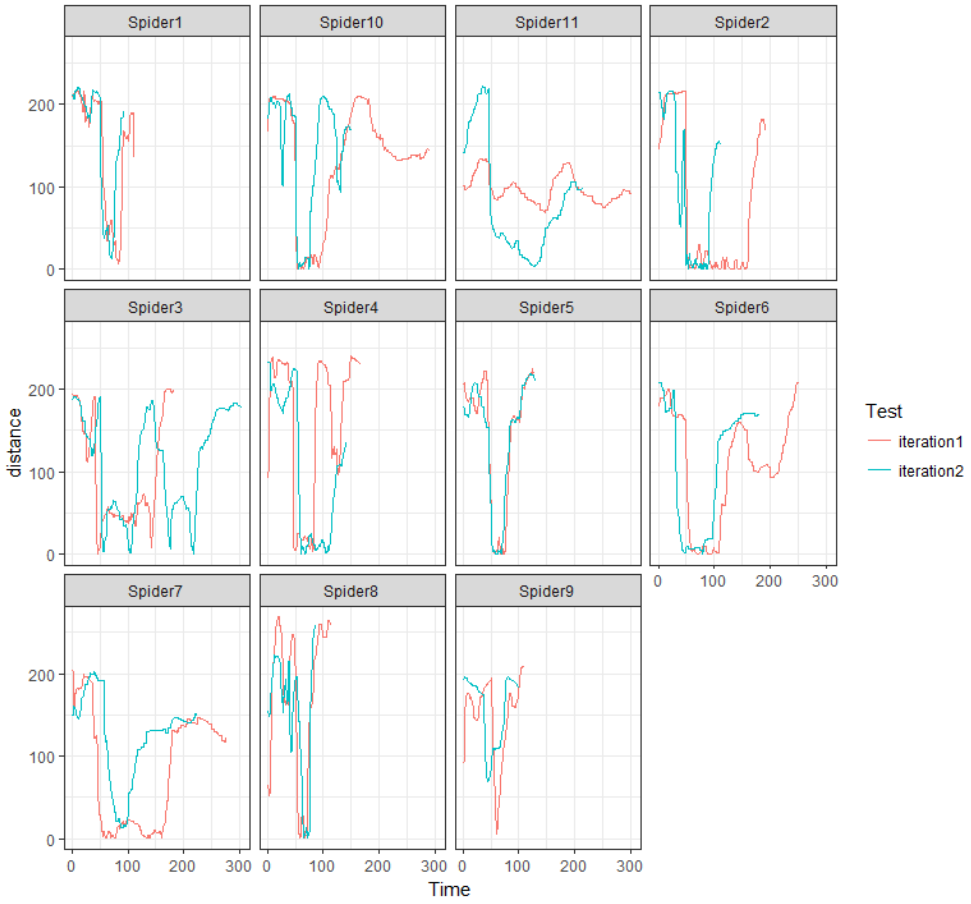
iteration2

iii.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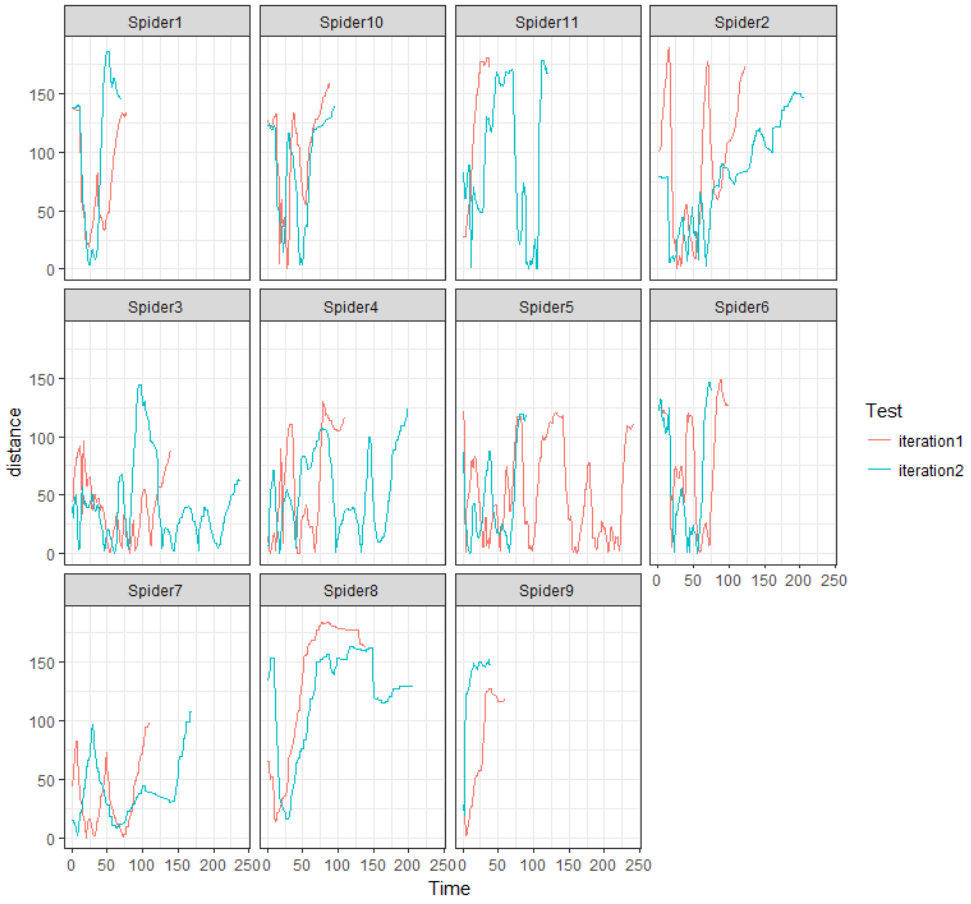
iteration1
iteration2

iv.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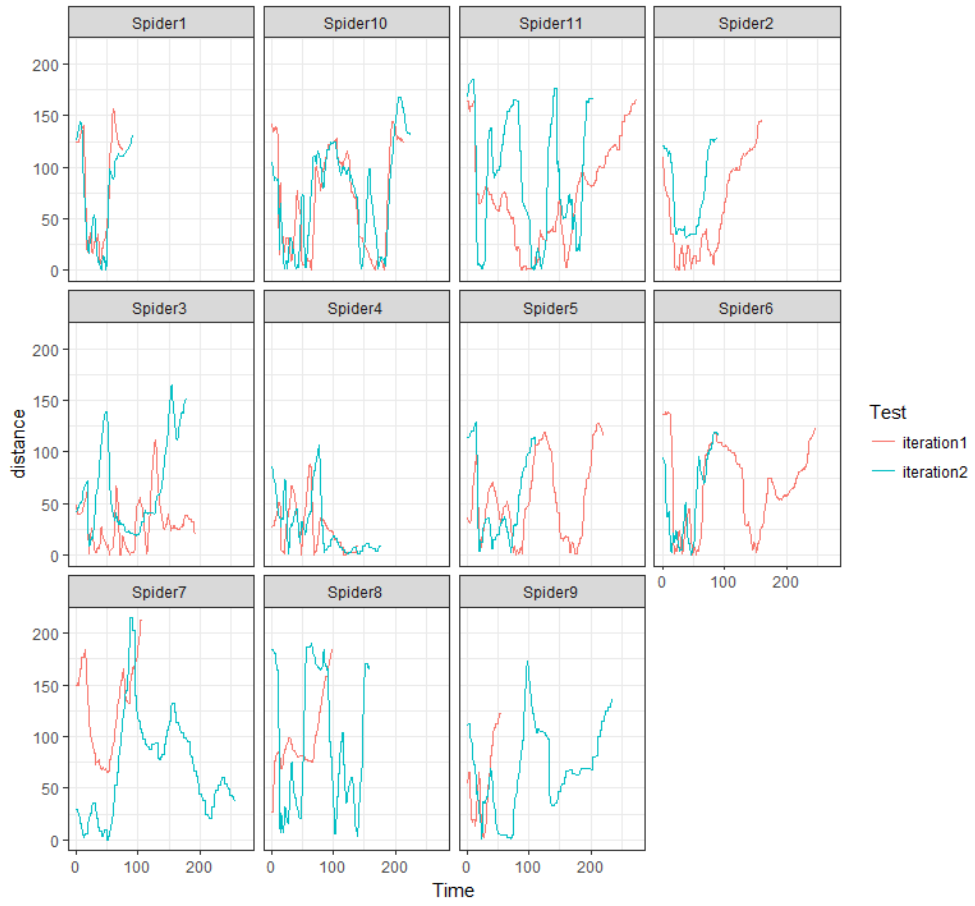
v.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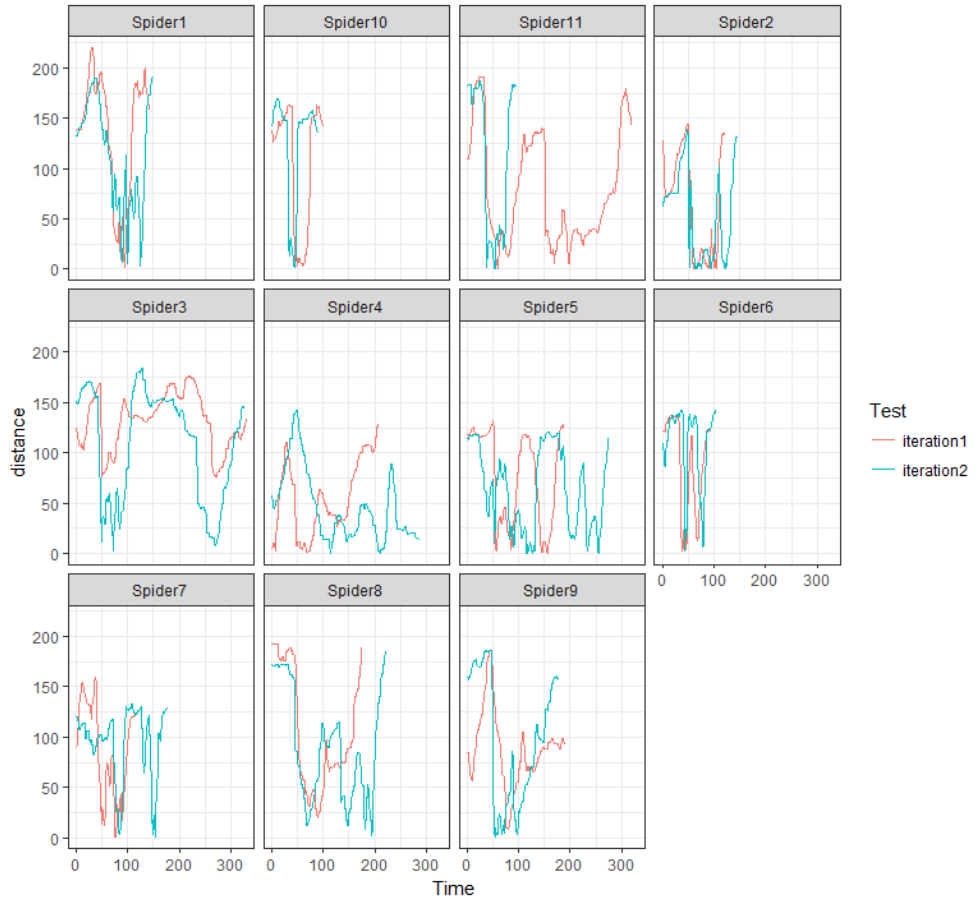
vi.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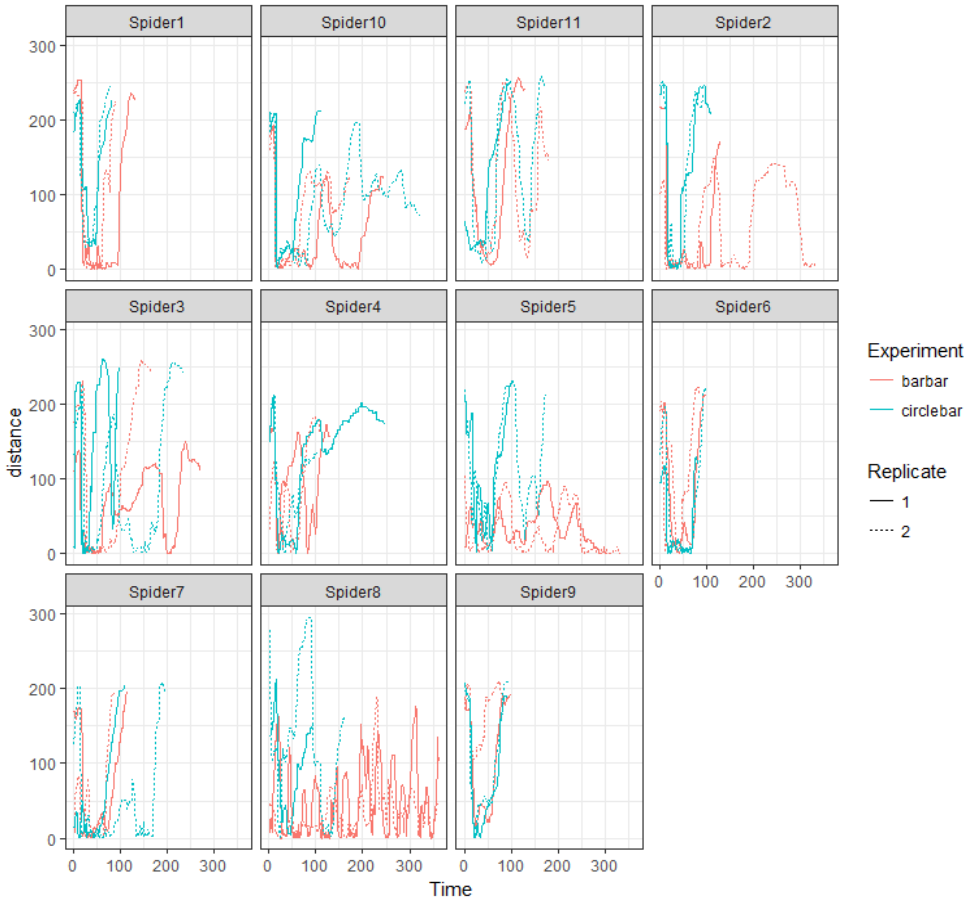
(B) i.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distance
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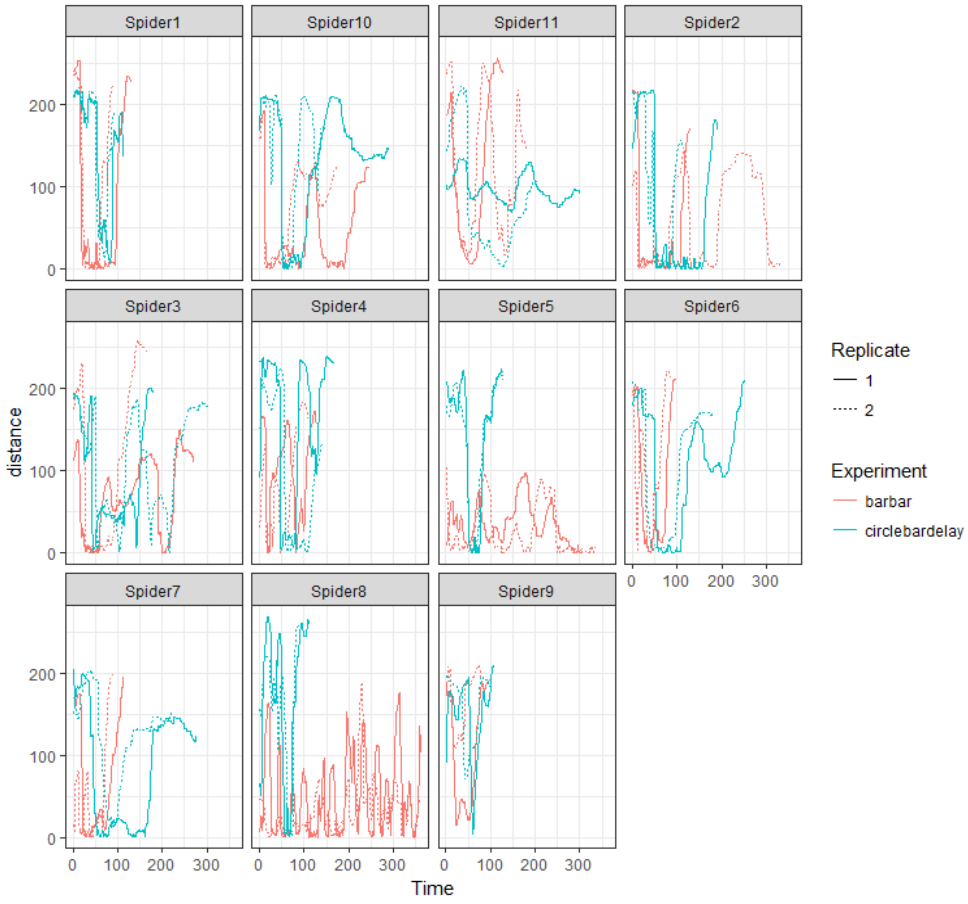
Experiment
barbar
circlebar
Replicate
1
2

ii.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Experiment
barbar
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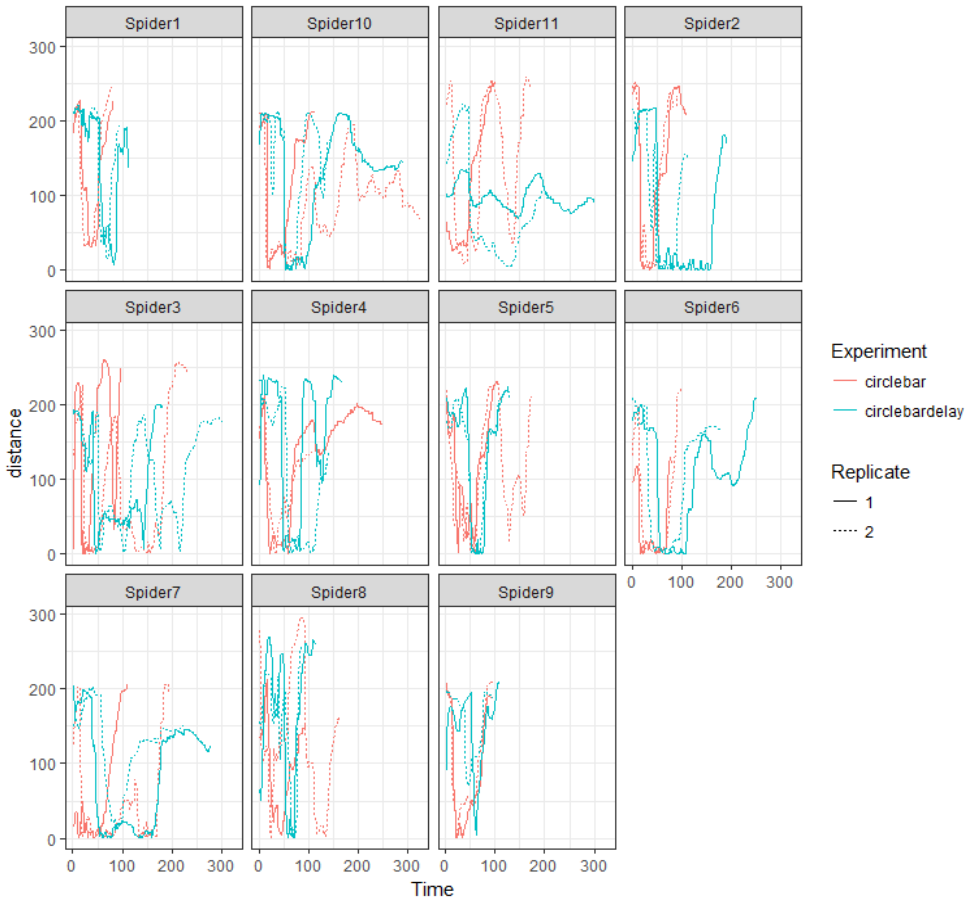
iii.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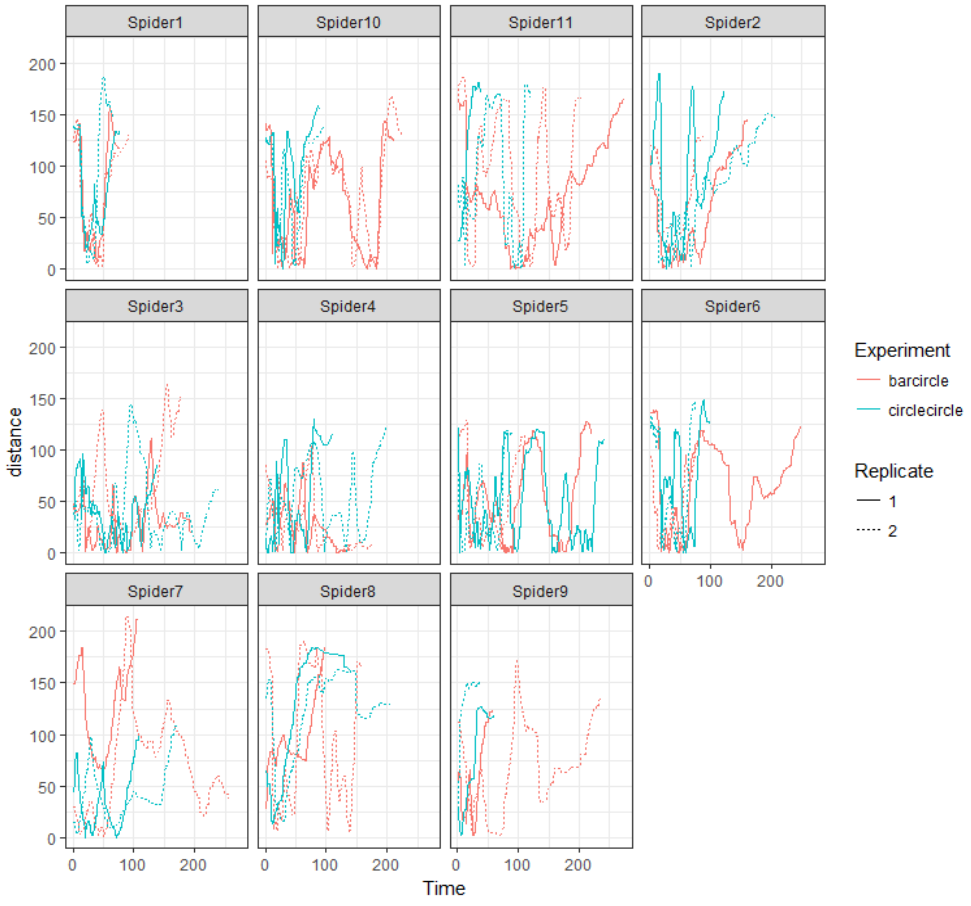
iv.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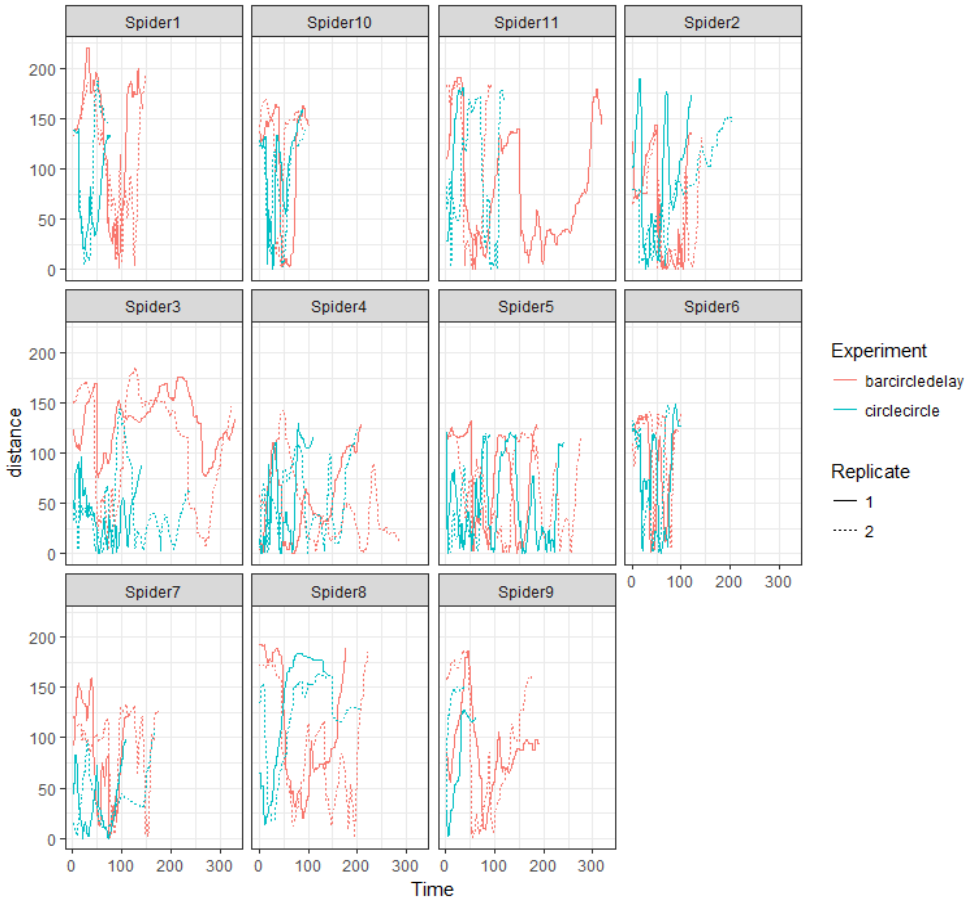
v.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vi.

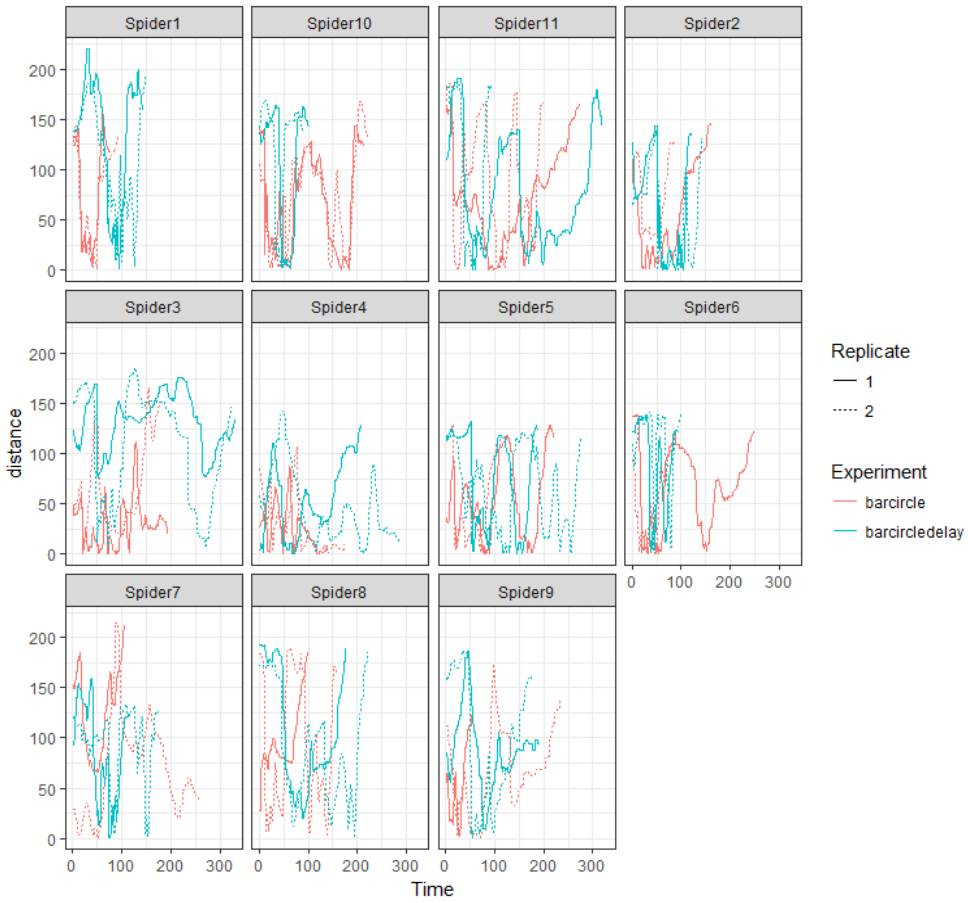

Figure 5. Distance in pixels from each point in a track to the edge of the main stimulus, plotted against time. Spiders 1 to 11 correspond to the spider identification number. (A) Comparing the distance measures between iteration 1 and iteration 2 for each paradigm. i. Bar-Bar. ii. Circle-Bar. iii. Circle-Bar Delay. iv. Circle-Circle. v. Bar-Circle. vi. Bar-Circle Delay (B) i-vi comparing both iteration 1 and 2 between the matched and mismatched paradigms; as well as the immediate and delayed paradigms. Replicate 1 and 2 represent iteration 1 (solid lines) and 2 (dashed lines) for each paradigm.

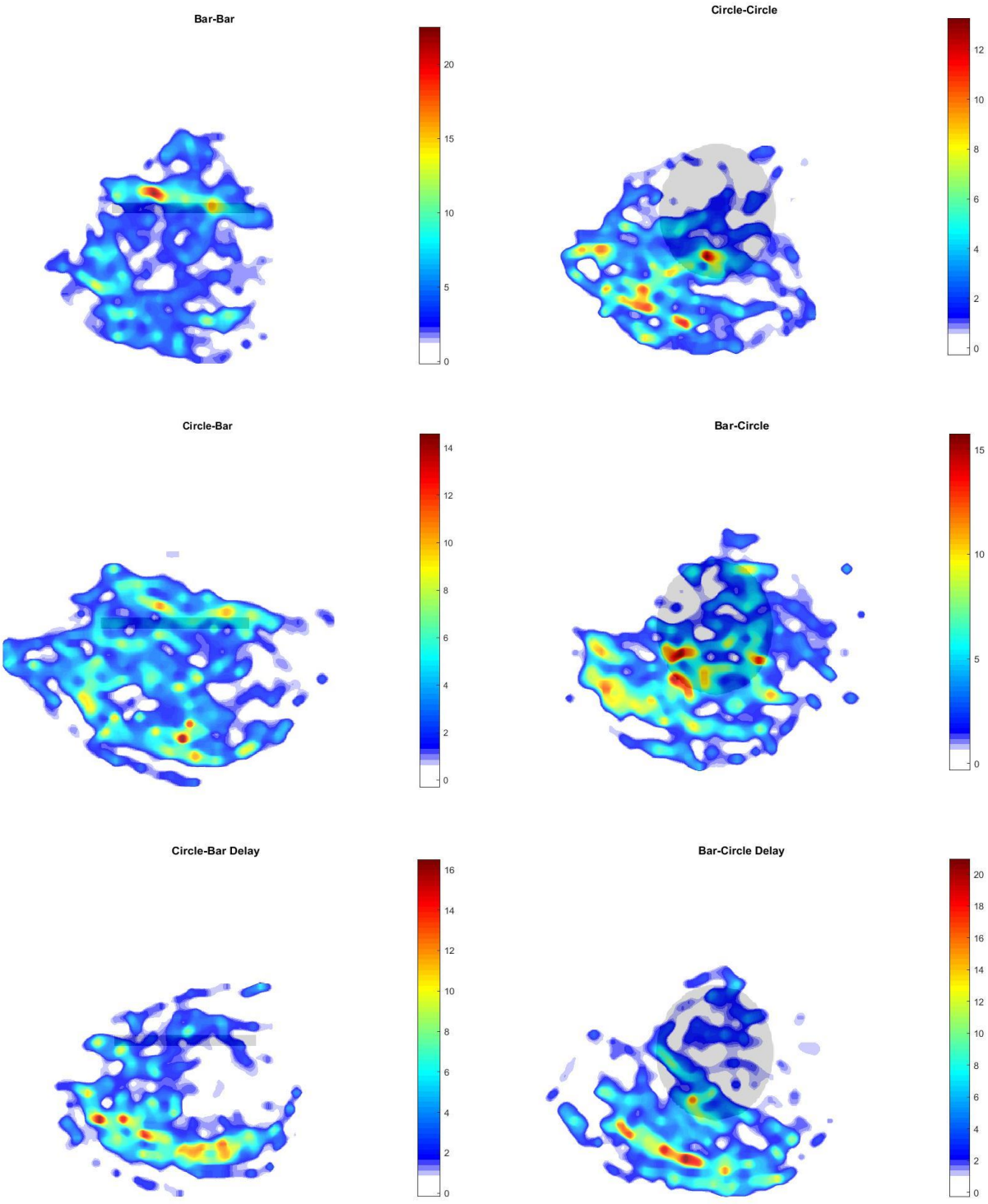

Figure 6. Scanning heatmaps for combined iteration 2 tracks. Main stimulus depicted in pale grey. For all paradigms n=11.

Discussion

My results clearly indicate that there is an effect of visual priming on the scanning patterns and scanning activity of the primary retina. Combined, the analyses all show changes in the scanning motion and increased activity of the primary retina in response to priming of the secondary eyes. Visual analysis of the tracks shows a clear pattern of priming in many of the spiders, especially in the circle-bar and circle-bar delay priming paradigms, while the combined heatmaps show a clear change in general scanning patterns in response to priming. In addition, the variation of the distance measures to the edge of the stimulus was significantly different for both delayed mismatched paradigms compared to the matched paradigms of the same main stimulus. Together, these analyses provide the first evidence of visual priming within the distributed visual system of salticids.

The results of the paired t-tests comparing the retinal activity of the tracks indicated that the two stimuli elicited different responses from the spiders. The bar stimulus had a strong effect in increasing the activity of the retina, as both a priming and as a main stimulus. This result is interesting, as it is expected that a circle would be a more biologically relevant shape in nature. For example, a circle could represent eyes, or body of another animal. That is not to say that salticids would not encounter rectangular shapes in their natural environment. Shape varies greatly across prey species (Bednarski et al. 2012) and some prey species may not be circular (Dolev and Nelson 2014). Even though salticids have highly acute vision (Jackson et al. 1990), Bednarski et al. (2012) found that even after learning, salticids were not able to differentiate between a moving rectangle and a video of a live cricket. However, praying mantises are significant predators of salticids (Nelson et al. 2006). Yet, it is possible that a bar is a much less common shape to encounter in nature, especially for this particular species, and so spiders may take a longer time to scan and process the image. This is because *M. marina* live on the rocky beaches (Jackson et al. 2006b). This species spends its life living amongst small stones and is therefore surrounded by roughly circular objects. It may be the case that for this species, a bar is a far more unusual shape and produces a longer and more careful scanning pattern as a response. It would be interesting to determine the responses of species living in dramatically different habitats to test this hypothesis.

While the bar stimulus has a less clear effect on the scanning patterns when primed, the priming bar stimulus did elicit a response by increasing the retinal activity. This indicates that the priming bar stimulus was perceived by the spider and any changes in the scanning patterns simply may not have been as obvious as the effects of the other priming stimulus. The scanning pattern with the circle stimulus often covered a wider area of the screen and was less targeted than the scanning patterns directed towards the bar. The typical horizontal scanning pattern used for the bar

may not stand out against the scanning patterns used for the circle. Whereas, the circle scanning patterns are much more obvious when compared to the horizontal scanning patterns of the bar.

The different responses towards the two stimuli may also have been due to experimental design rather than biological relevance. Behavioural tests suggest that, when looking at an object, salticids focus on the edges and do not often look at the entire object (Tedore and Johnsen 2016). Therefore, when creating the stimuli, special care was made to keep the edge size of the two stimuli similar. The ratio of the circumference of the circle compared to the perimeter of the bar is 9:8. However, the circle is much larger than the bar, with the area of the two stimuli being 13:1. The large size difference may change the behavioural response of the spiders. The forward-facing anterior lateral (AL) eyes are responsible for responding to looming objects (Spano et al. 2012) and the immediate appearance of the large circle in the field of view of these secondary eyes may resemble a predator and affect the subsequent scanning response of the primary eyes. If spiders are responding to a possible threat, they may spend less time scanning the object in front of them. This could explain the lower retinal activity in response to the circle stimulus.

In many of the tracks, the second iteration had a stronger effect of priming. This was particularly apparent when the circle was the priming stimulus. In most instances, scanning pattern of the retina was much more circular in the second iteration than in the first. This is probably due to working memory and learning effects. Working memory has been extensively studied in vertebrates, including dogs where working memory lasts for at least 240 s (Fiset et al. 2003), and rats (Morris 1984, Bimonte-Nelson 2015). Working memory has also been demonstrated in invertebrates such as honeybees (Brown and Demas 1994) where spatial working memory is used to track which locations have been visited previously whilst foraging. Furthermore, research by Cross and Jackson (2014) has shown that working memory is retained by salticids for at least 90 s.

Additionally, the stronger effect of priming perceived in the second iterations may also be due to repeated exposure of the priming stimulus. Priming is improved with increased exposure to the primed object (Wiggs and Martin 1998, Bond and Kamil 1999). Between each iteration there was only a two minute interval, in which it is likely the spiders retained a lot of visual information from the first iteration. Therefore, the repeated exposure to the priming stimulus after the second iteration may also explain why priming had, in most instances, a stronger effect on the scanning patterns during the second iteration compared to the first.

Working memory is subject to capacity limitations (Goto et al. 2014); especially as salticids have very small nervous systems (Carvell et al. 2017). Differences between the immediate and delayed unmatched paradigms can give us an indication into the neural processes involved during priming. The delayed paradigms were significantly different to the matched paradigms when

comparing the distance of the track to the edge of the stimulus. This indicates that the 500 ms delay is increasing the effect of priming on the retinal tracks. The difference between the immediate and delayed paradigms could be due to the time it takes for the nervous system to compute the task (Chittka and Spaethe 2007), due to the number of neurons and synapses involved (Medan et al. 2015). Information from the secondary eyes must travel from the eyes, through to the central nervous system for processing and a response enacted upon from there through to the motor neurons controlling the primary retinae (Hill 1975). These results suggest that the extra 500 ms involved in the delayed paradigms was enough time for the nervous system to process the priming stimulus before the presentation of the main stimulus, but that the immediate paradigm was too soon. Further suggesting this hypothesis that sometimes it was at the end of the presentation of the main stimulus, that the priming effect of the priming stimulus (when mismatched) became evident, especially in iteration 1.

I found a large amount of variation in the scanning patterns between spiders. However, there was far less variation within individual spiders. If scanning patterns in salticids is learned, then this could explain the large variation in scanning patterns between individuals. In humans, scanning patterns are learned and individuals must learn the best patterns of movement to gain the optimal information (Hayhoe and Ballard 2005).

It is important to note when analysing these data, that the field of view of the AL eyes entirely overlaps the field of view of the primary eyes (Zurek et al. 2010, Zurek and Nelson 2012a). When the main stimulus is presented to the spider, the spider is able to perceive the image in its entirety, in lower resolution, with the AL eyes (Zurek et al. 2010). The AL eyes can visually guide the scanning patterns of the primary retina, while also gaining some spatial details themselves.

In most vertebrates, it is widely accepted that the centre of the retina is used as the focus of attention (Hazan et al. 2015). This is also true for salticids, as the centre of the retina has the highest density of photoreceptors and is often used in feature detection (Land 1969b). Therefore, I chose to track the retina from this point. However, spiders do occasionally use the edges of the retina when scanning over an object. I did not record instances where the edge of the retina was being used to scan the object, but in my data, there are instances where the tracked point of the retina was not over the stimuli, but the spider would still be viewing the image with the edges of its retinae. The reasons why a spider would choose to scan an image with the edges of its retinae, with its larger and less densely-packed photoreceptors are not known. It would be interesting to track the edges of the retina to try and see when and why they use this area of their retina when scanning an object.

While this research is the first time visual priming has been studied in a salticid visual system, it is not the first time expectation violation experiments have been used to study behaviour

in salticids. Cross and Jackson (2017) studied numeracy in *Portia*. Spiders were placed on a detour in which prey were visible at both the beginning and end of the track. When spiders were out of sight of the prey, the number of prey was manipulated. Cross and Jackson (2017) found behaviour towards the prey changed when expectation was violated. Expectation violation studies have also been used in working memory studies, in which the attack frequency of salticids changes when expectation is violated (Cross and Jackson 2014). While both studies used behavioural responses to assess the effect of expectation violation, the results are interesting to compare to my results. All studies, whether on the decision-making of the spider or of the retinal scanning patterns (here) show that priming influences how salticids assess objects in their environment.

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Chapter 3:

Discussion

Birdling's flat: Typical habitat of *Marpissa marina* (Photo: L. Scott)

Discussion

In this thesis I investigated the effects of visual priming between two pairs of eyes in the distributed visual system of a New Zealand jumping spider, *Marpissa marina*. The aim of this research was to see whether the secondary eyes, specifically the posterior lateral eyes, were involved in visual processing of shape information to prime the retinae of the primary eyes. My results indicate that the secondary eyes are in fact providing shape information to the primary eyes; thereby facilitating the scanning patterns of the primary eyes and leading to more targeted scanning patterns. In nature this is likely to cause the spider to make faster and more accurate decisions.

Many areas of this research were challenging, from setting up the spiders and calibrating them so that the retinae were in full view in the eye tracker and the spiders being responsive, to the data analysis. For the method of data analysis chosen, I calculated the distance from each point in the tracks to the edge of the main stimulus. These distance measures were then plotted against time and analysed using a generalised additive mixed effect model. The plots were then averaged to calculate the general trend of the data for each paradigm. However, one pitfall of this method is that, when averaging out the distance estimates across all spiders, the extreme points of information are lost. These points may provide some interesting information, i.e. when the spider is focusing on the edge of the stimulus (when the fovea of the retina is scanning the edge of the stimulus, the distance from the tracked point to the edge will be close to, or equal to zero).

One possible future method of analysis is to categorise points of the track into close or far from the stimulus edge. A proportion of the points close to the stimulus can then be modelled as a binomial mixed-effect model. The benefit of this method is that the 'extreme' information in the data is kept, such as when the spider is scanning the edge of the stimulus, both with its fovea, or with one of the 'arms' of the boomerang-shaped retina. This would lead to a similar analysis as seen with eye-tracking experiments done with vertebrates (Meeter and Van der Stigchel 2013, Yorzinski et al. 2013). However, most vertebrates such as humans, monkeys and birds, typically have saccade and fixate patterns of eye movements (McPeek and Keller 2001, Brychtova and Popelka 2012, Yorzinski et al. 2015), which differ from the salticid scanning patterns. One major limitation in analysing salticid retinal movements this way would be the loss of pattern information across time when transforming the continuous scale distances to a binary decision. For this research, I was most interested in the changes in scanning patterns due to priming, and thus I was interested in how scanning patterns changed over time, which was why I ultimately chose against this method of analysis.

Priming of behaviour has been previously demonstrated in salticids, yet the effects of priming varies across species. Cross et al. (2007) studied the effects of female olfactory cues in male-male interactions in seven species of salticid, including *M. marina*. However, they did not find evidence of priming in all species; in only two of the seven species tested, male-male conflicts escalated after being primed with female odour (Cross et al. 2007). This may suggest that we cannot assume that visual priming will influence the behaviour of all species of salticid equally.

I chose to exclusively test female *M. marina*, as female salticids are more willing to complete behavioural tasks than males (Zurek et al. 2010). Female and male salticids differ significantly in their behaviours. Females are more effective hunters (Li and Jackson 1996), feed more often than males (Zurek et al. 2010), and are more prone to cannibalism (Jackson et al. 1990). Whereas males spend most of their time courting and searching for mates (Jackson and Pollard 1996, Liedtke and Schneider 2017). Even though I only tested females in a single species, I found a large amount of variation in the scanning patterns between individuals. It would be interesting for future research to investigate possible sex differences in scanning patterns.

Jumping spiders are known for their exceptional vision (Forster 1979, McGinley and Taylor 2016). However, the visual system of salticids varies substantially across species. *Portia*, for example, has the highest spatial acuity of any salticid species (0.04°) but *Phidippus johnsoni*, a species with a more typical visual system, has a spatial acuity of 0.13° (Harland et al. 2012). While the spatial acuity of 0.13° is immensely impressive for such a small animal, the acuity of *Portia*'s eyes are still three times better than *P. johnsoni*. Additionally, habitat also influences the evolution of visual systems (Hu et al. 2014). In particular, light conditions affect the retinal design and spectral transmission of the cornea (Blest 1985, Hu et al. 2014), which, in turn, can subsequently affect the evolution of behavioural repertoires (Blest 1985).

The family Salticidae is the largest family of spiders (Jackson and Pollard 1996, Cross and Jackson 2017) and live in every type of non-polar, terrestrial habitat (Li and Jackson 1996). All salticids are predators (Raška et al. 2017), yet their diet varies considerably across species. Most species of salticids feed primarily on insects and are generalist predators (Tarsitano and Jackson 1992), as is likely the case with *M. marina* (Tarsitano and Jackson 1994). However, specialised prey preferences have evolved in several species. *Portia* is a genus of araneophagic salticids which prey on spiders (Tarsitano et al. 2000) and one species, *Portia fimbriata*, not only preys on web-building spiders but specifically searches out and hunts other species of salticid as its preferred prey (Harland and Jackson 2002). Being even more particular, *Evarcha culicivora* is a species with a preference for blood-fed mosquitoes in the genus *Anopheles* (Dolev and Nelson 2014). Another mosquito-specialist, *Paracyrba wanlessi*, has a preference for mosquitoes of all life-stages (Jackson et al. 2014). While many salticid species avoid ants (Jackson and Pollard 1996, Nelson and Jackson 2006), some species

have actually evolved preferences towards eating ants (Jackson and Olphen 1991, Jackson and Nelson 2012). This shows how diverse the predatory behaviours of salticids are throughout the whole family, and suggests that there might be concomitant effects in their visually-based decision making, as found by (Dolev and Nelson 2014) when comparing the responses of *Evarcha culicivora* with those of a generalist predator when assessing 'stick-like' representations of different types of prey, including mosquitoes (the referred prey of *E. culicivora*).

Marpissa marina lives in the rocky shore of New Zealand beaches. It is extremely likely that this habitat has strongly influence the evolution of their behaviour. Unfortunately, due to New Zealand's depauperate salticid fauna, no other species of salticid shares the same habitat as *M. marina* (Jackson et al. 1990) and so we are unable to test any other species which have evolved under the same environmental conditions. It is likely that this effect of priming reported may differ across salticid species, as does behavioural priming. It would be of interest to test species from different habitat types, evolutionary histories, and range of predatory behaviour to see how the behaviour of their visual systems differ across species.

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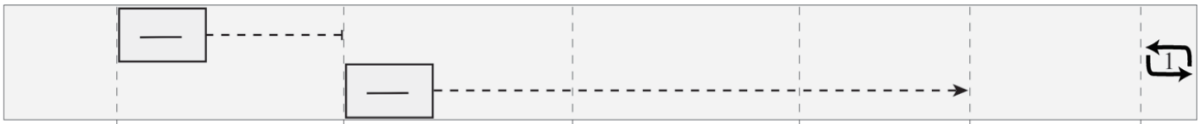
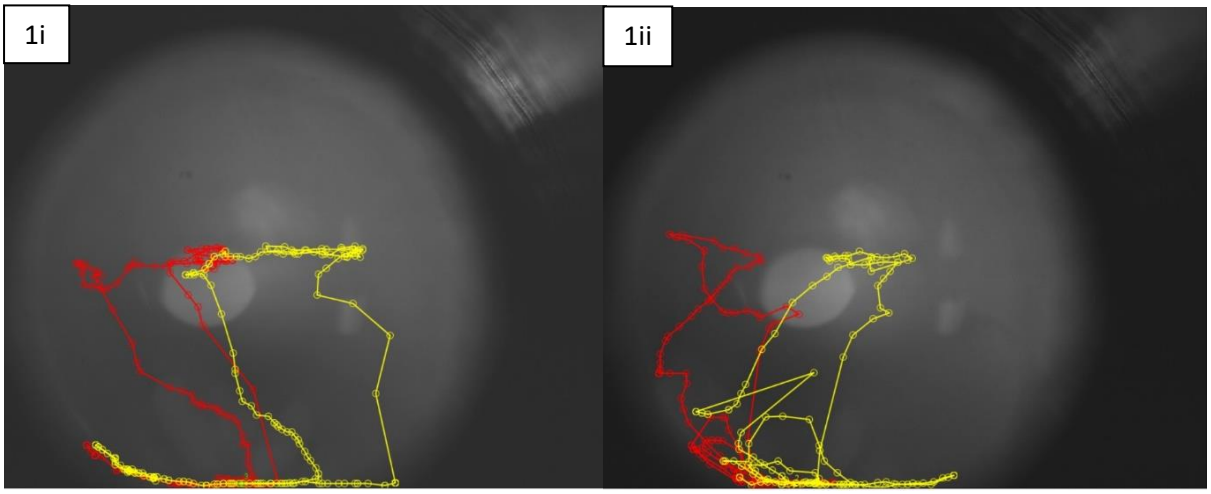
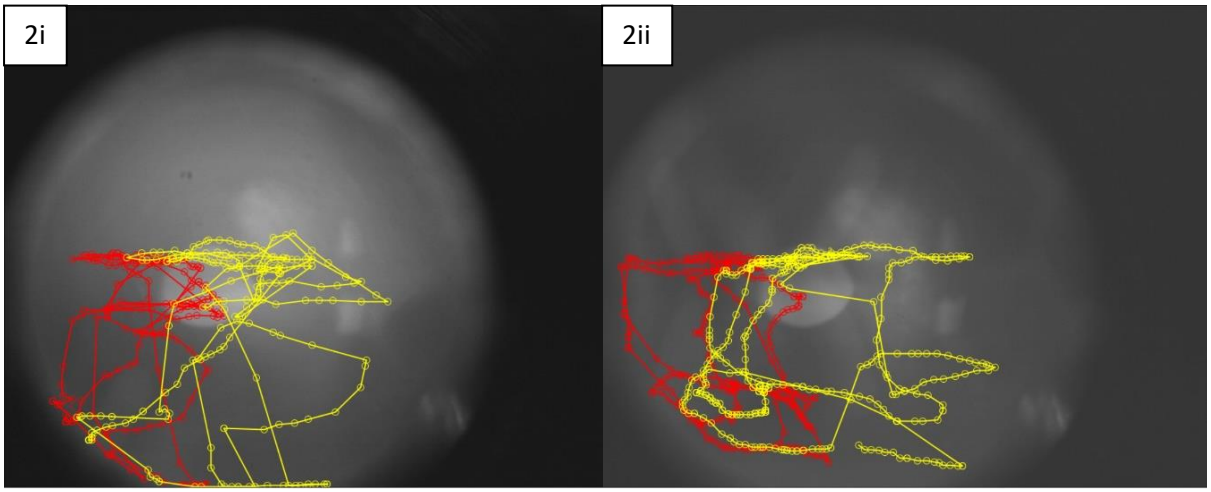
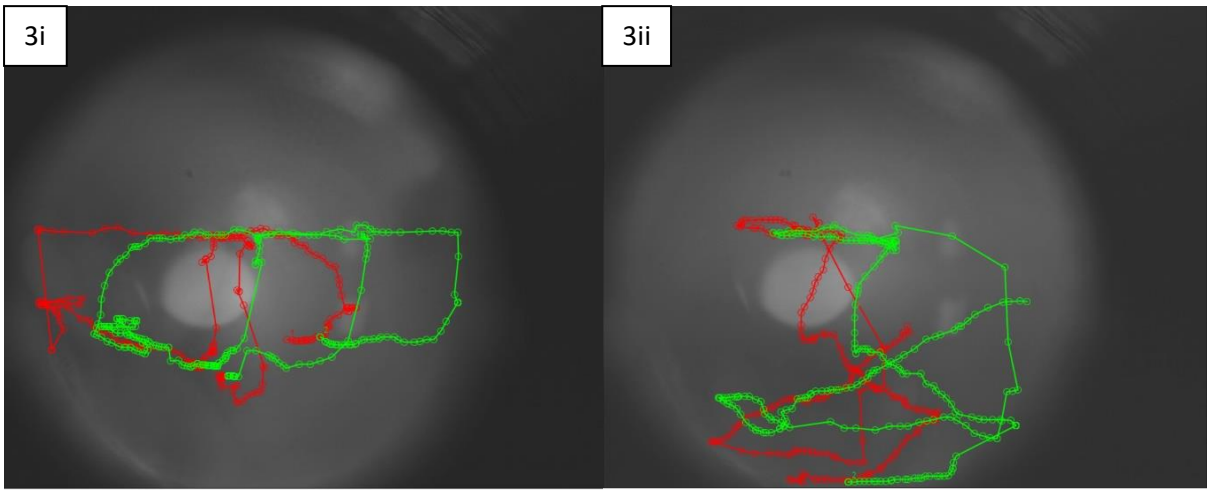
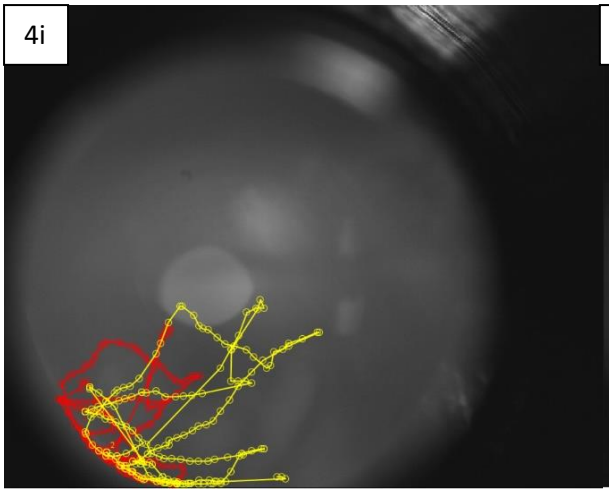
Appendix 1
Bar-Bar Tracks







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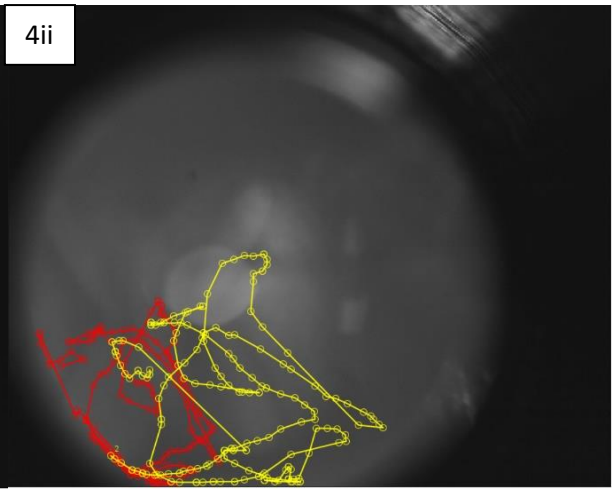
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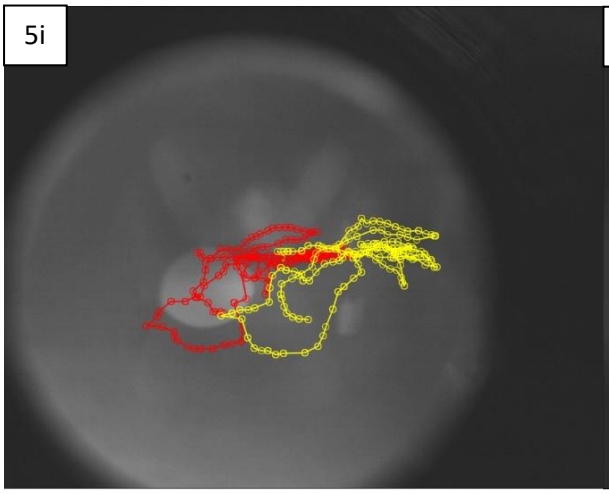
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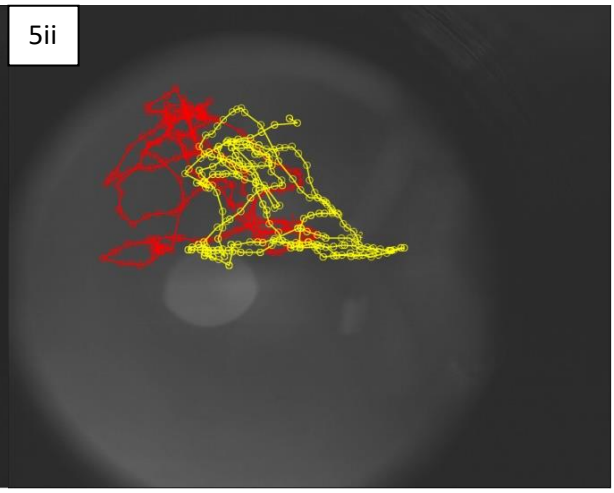
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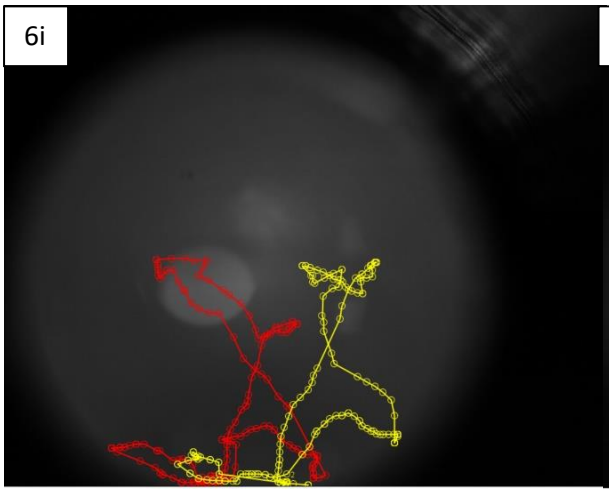
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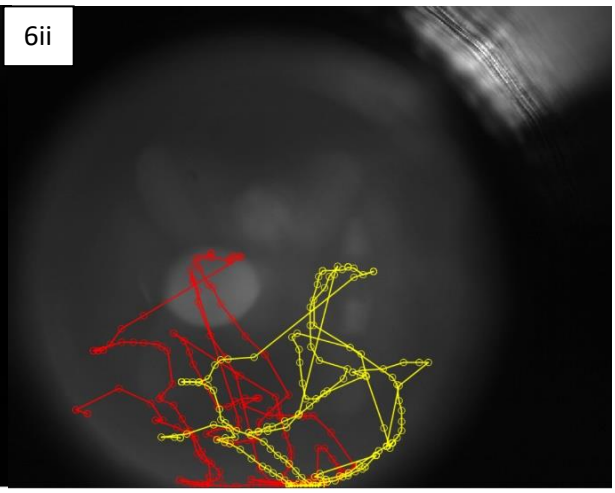
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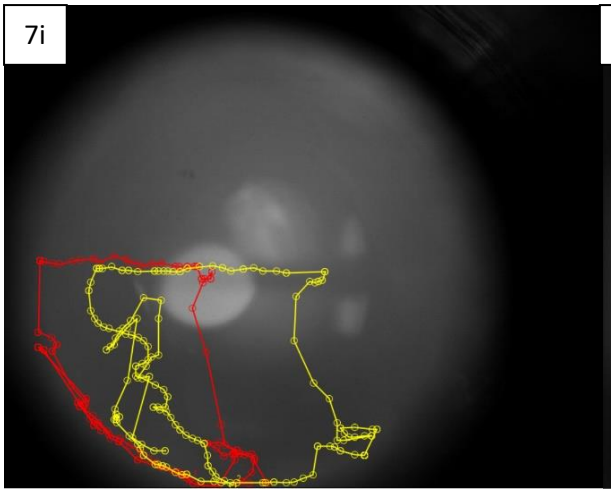
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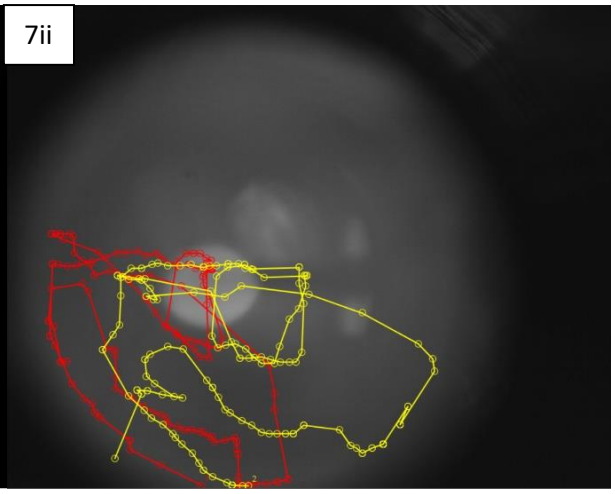
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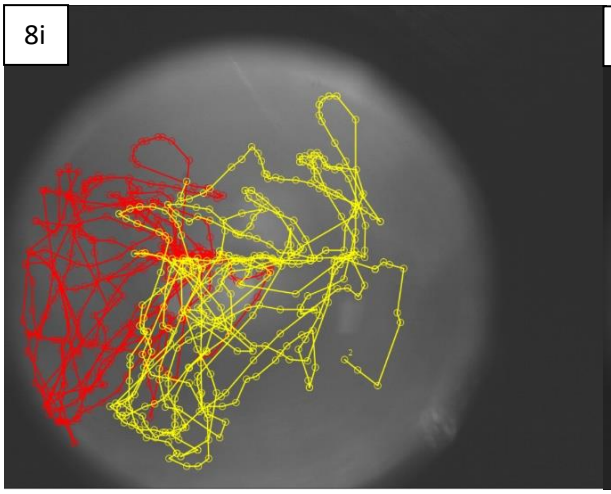
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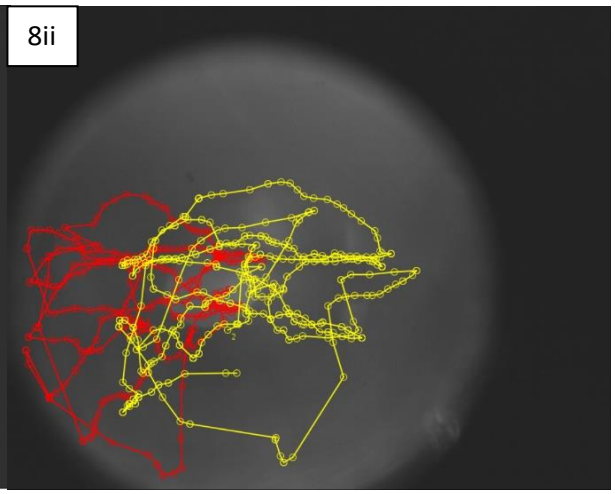
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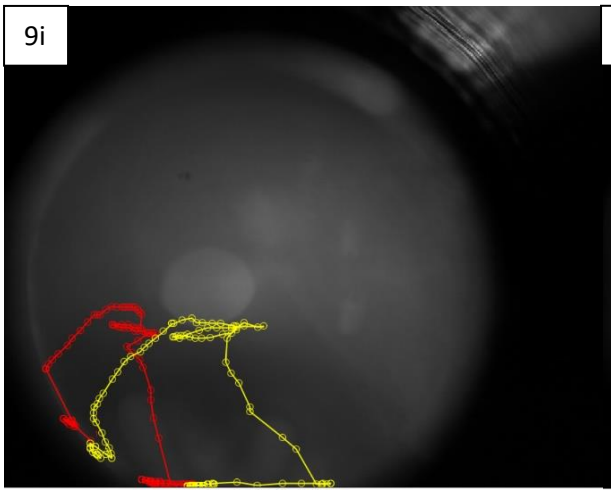
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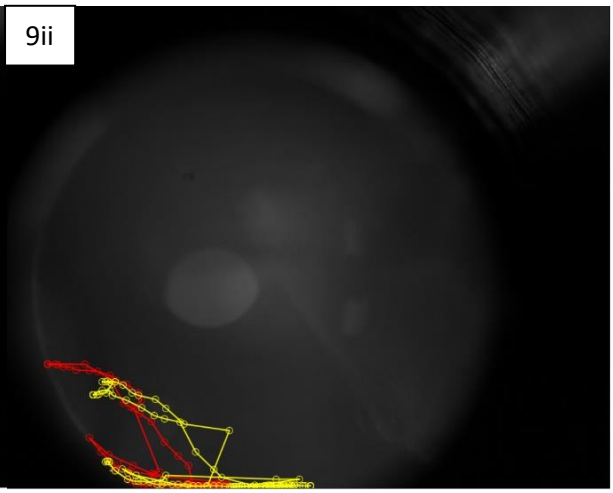
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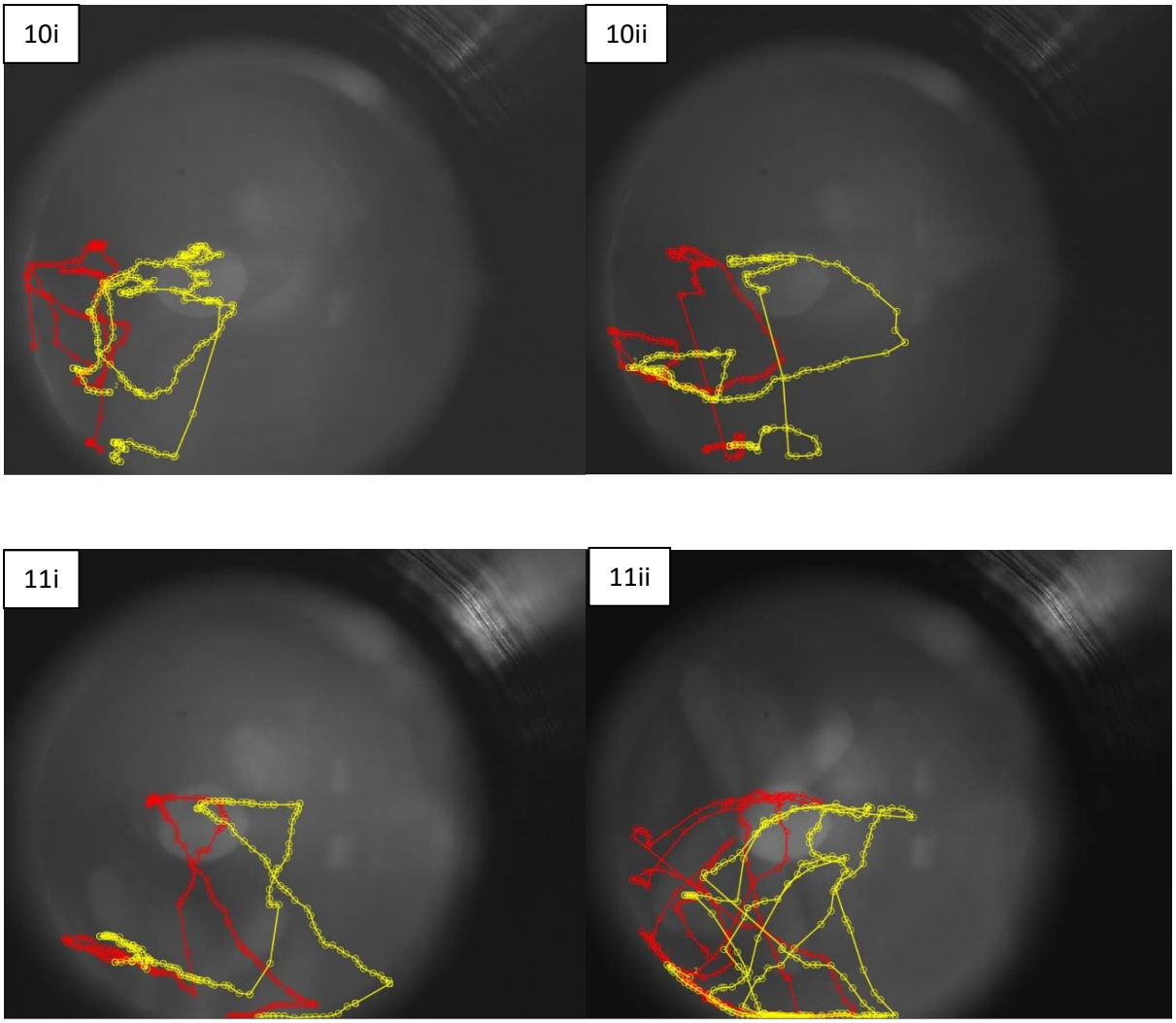
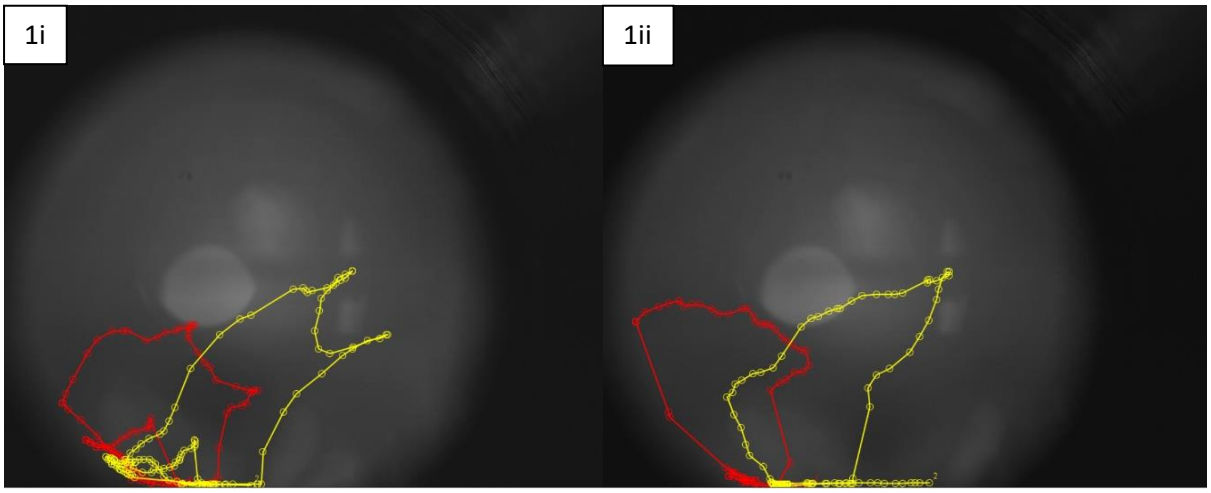
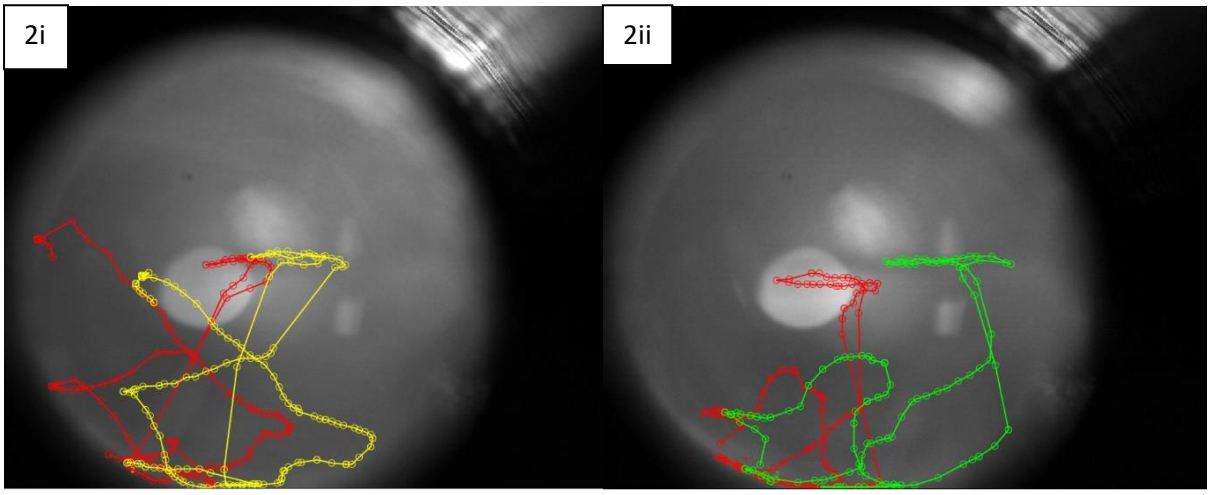
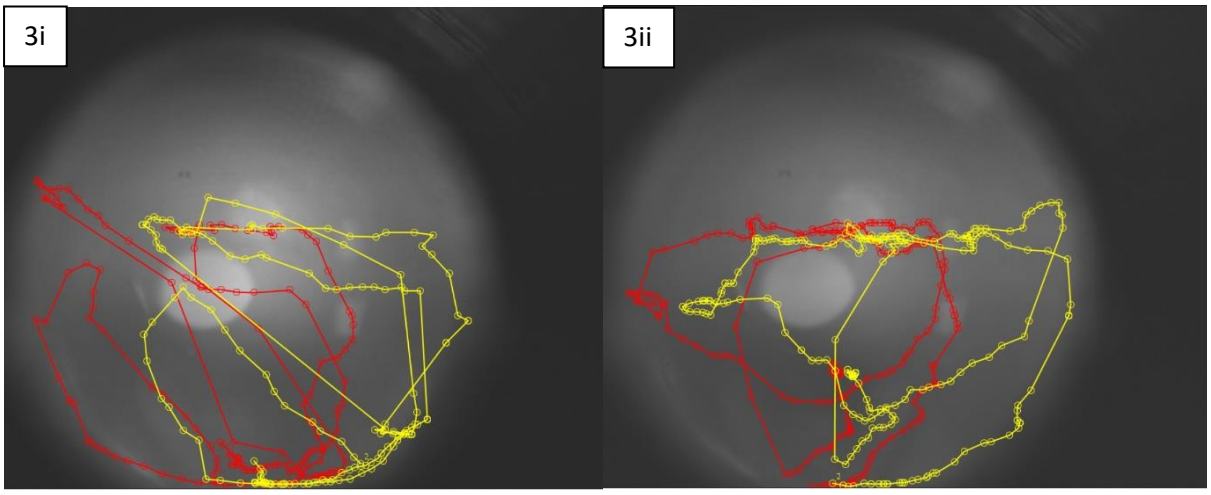


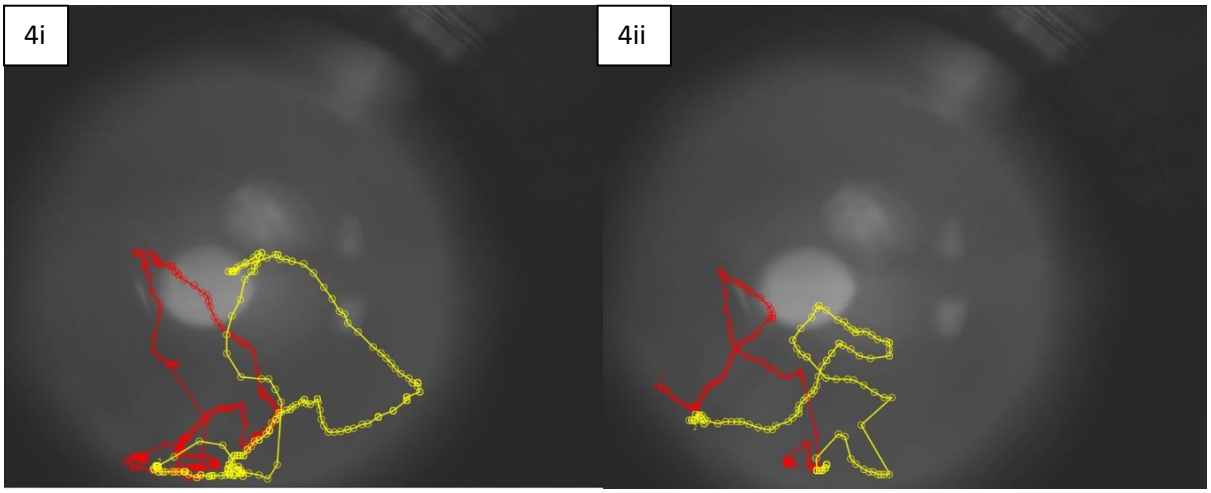
Figure 1. Raw tracks from the primary retina in response to the bar-bar priming paradigm. Each point refers to the centre of the retina. Red: Right retina. Yellow/Green: Left retina. Numbers 1-11 indicate the spider identification. i. Iteration 1. ii. Iteration 2.

Circle-Bar Tracks





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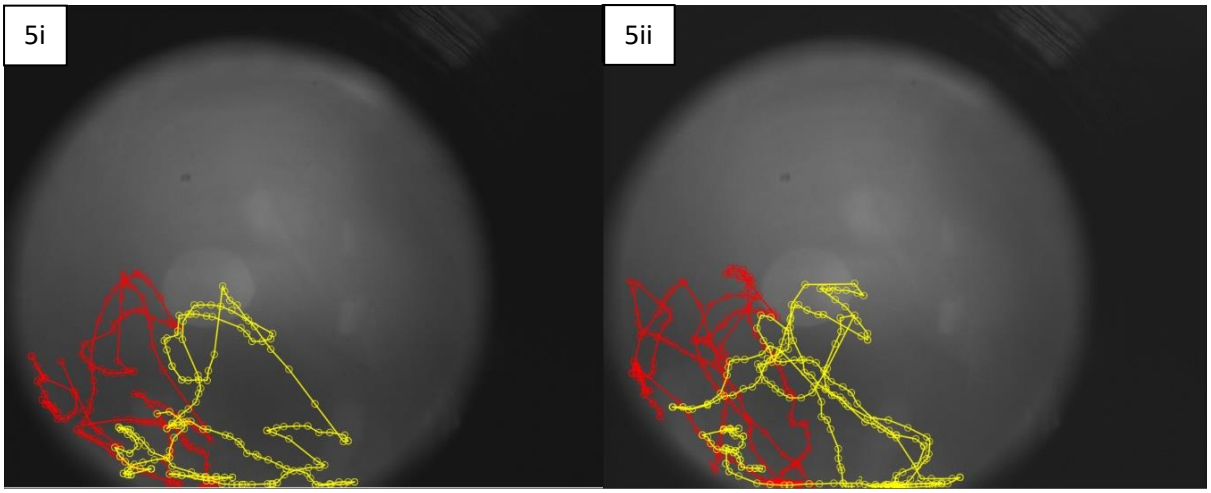
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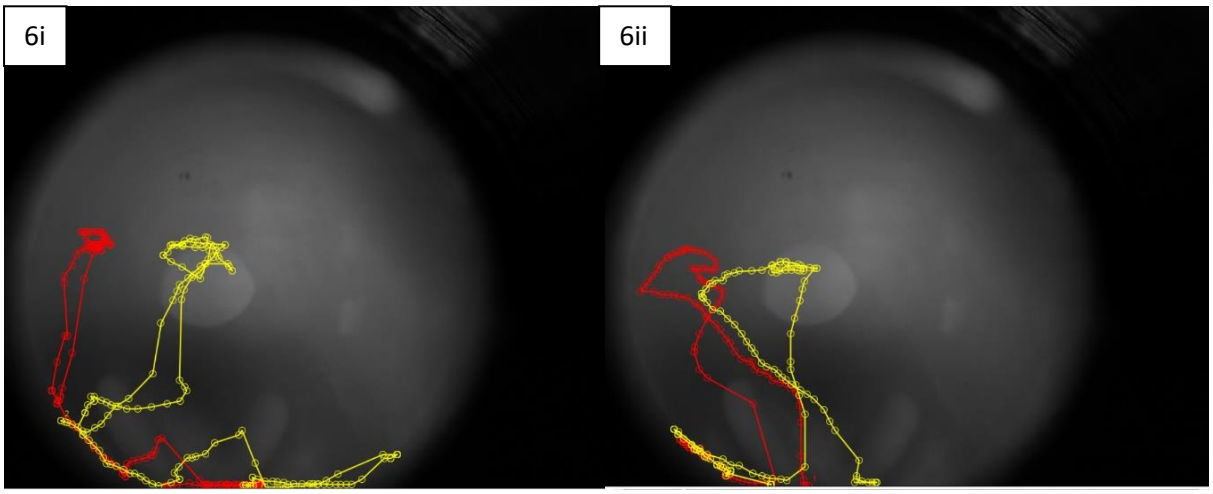
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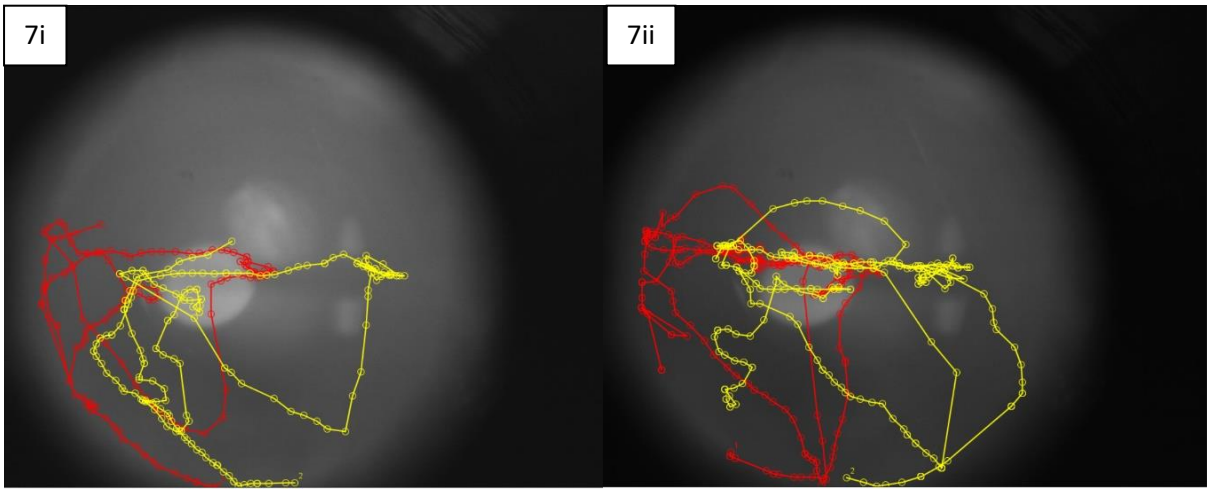
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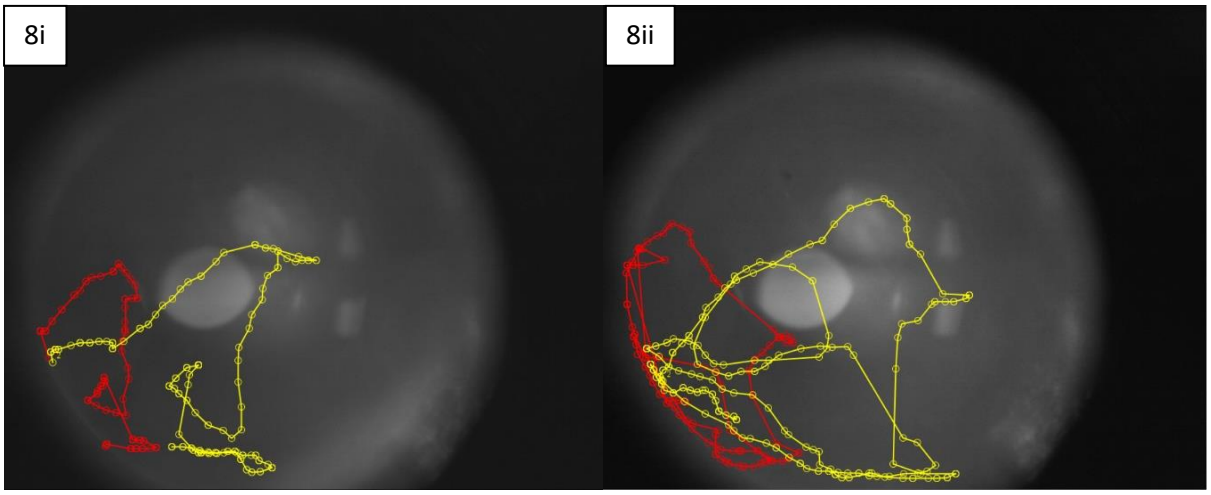
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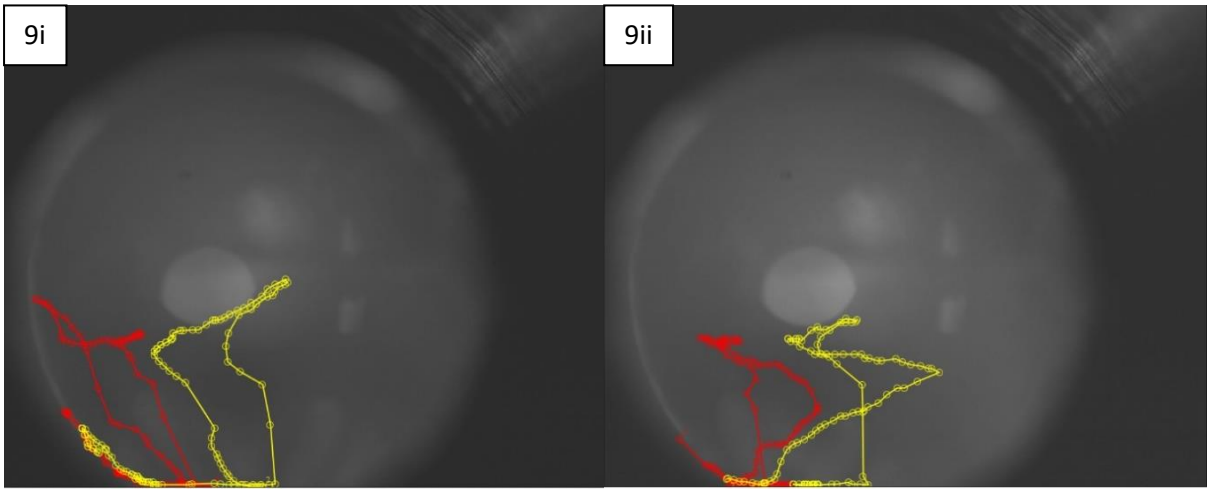
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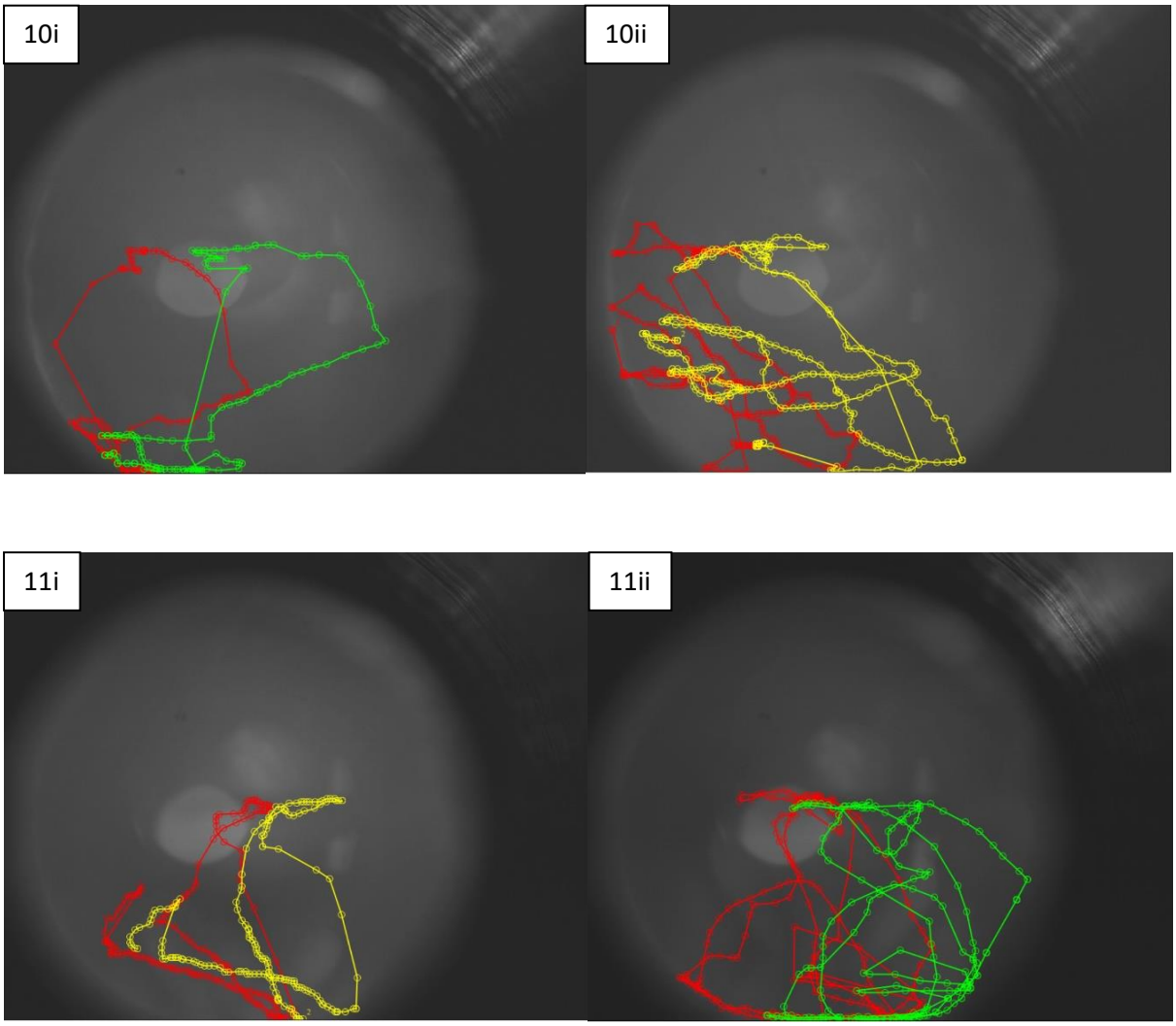
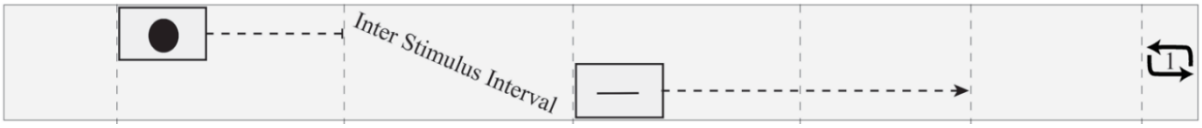
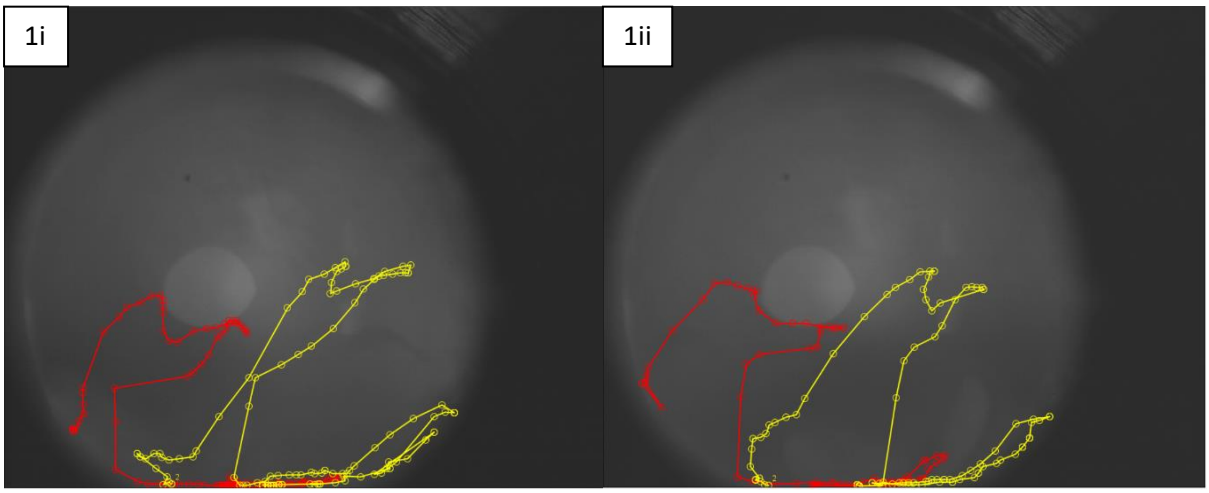
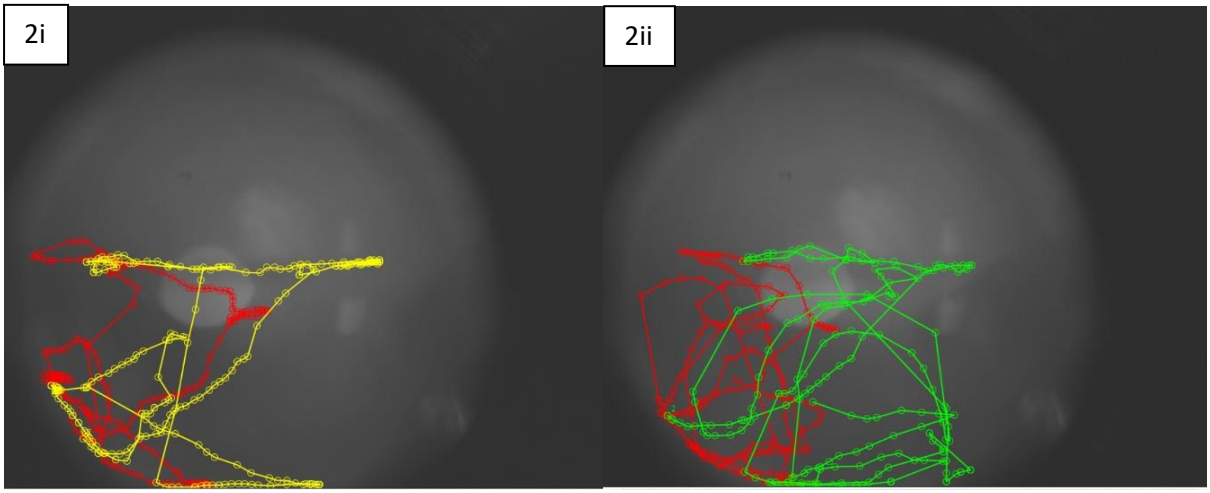


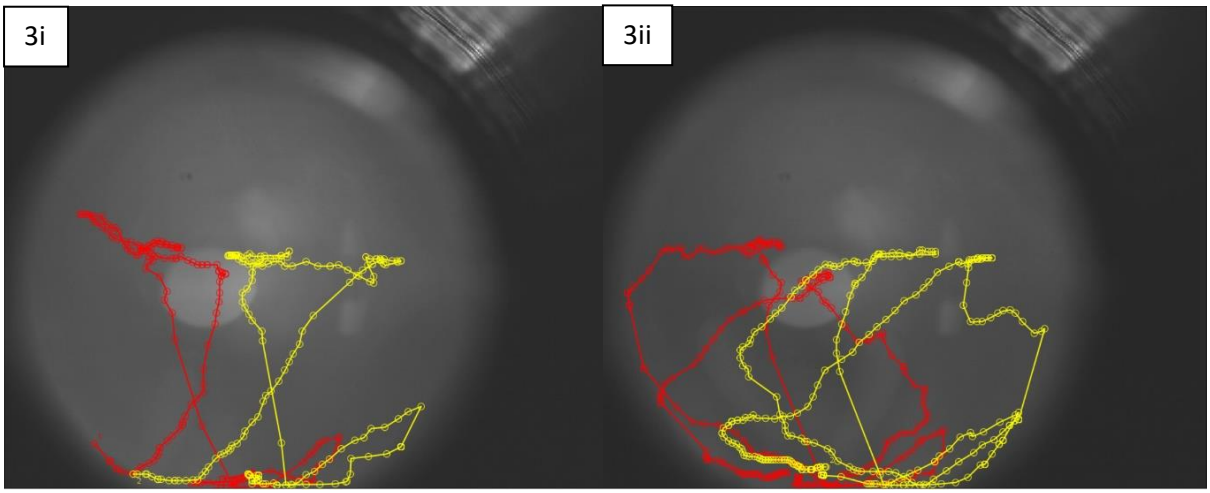
Figure 2. Raw tracks from the primary retina in response to the circle-bar priming paradigm. Each point refers to the centre of the retina. Red: Right retina. Yellow/Green: Left retina. Numbers 1-11 indicate the spider identification. i. Iteration 1. ii. Iteration 2.

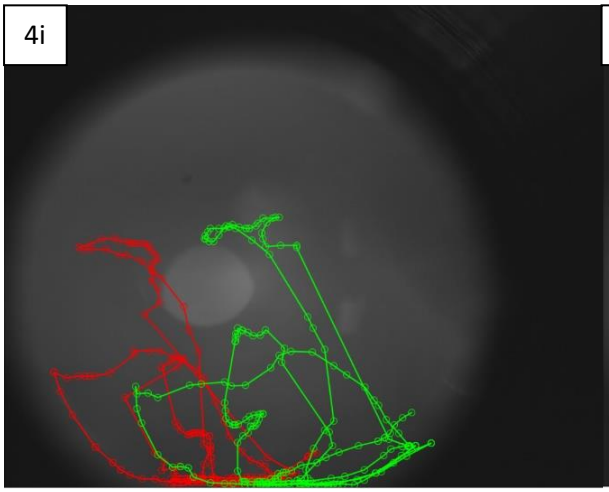
Circle-Bar Delay Tracks







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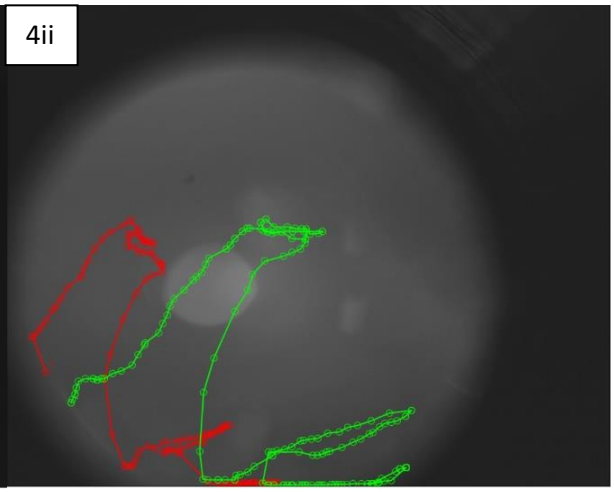
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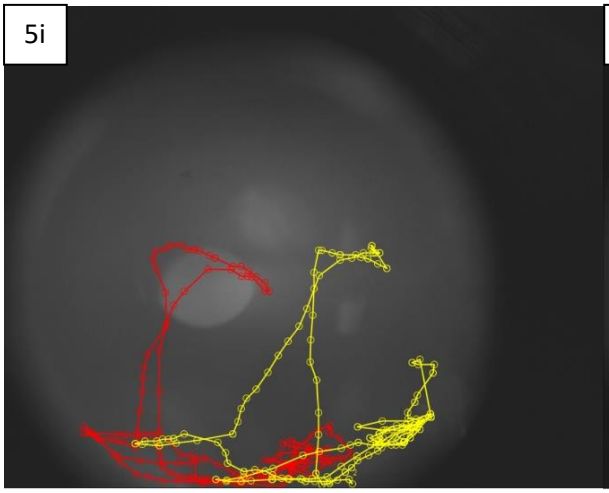
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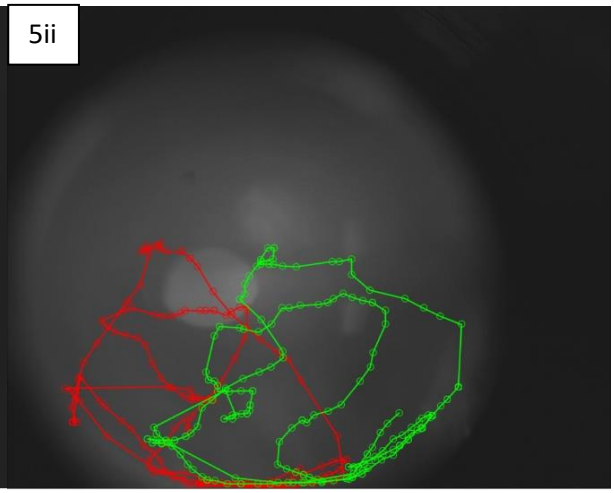
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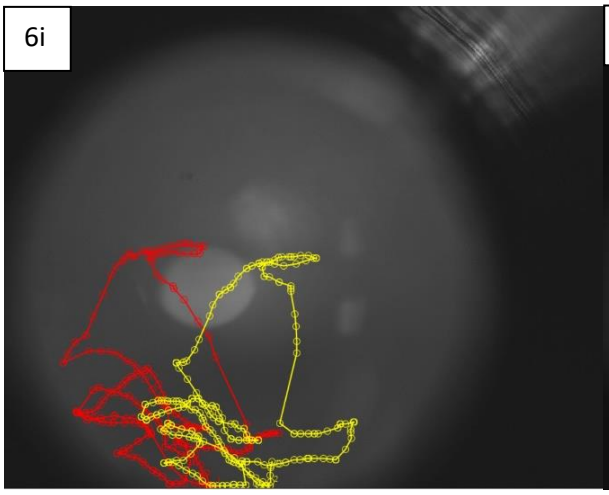
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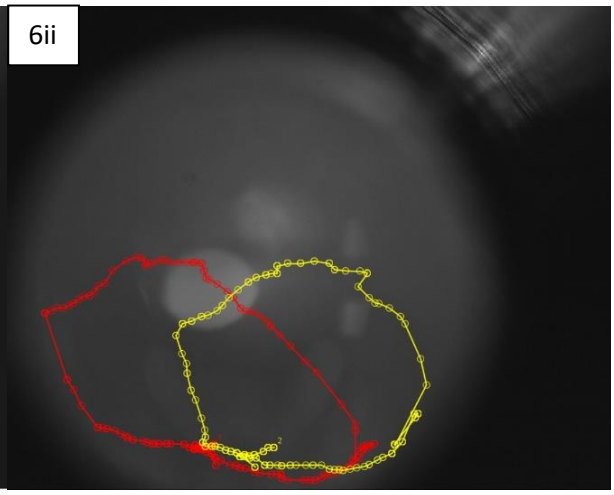
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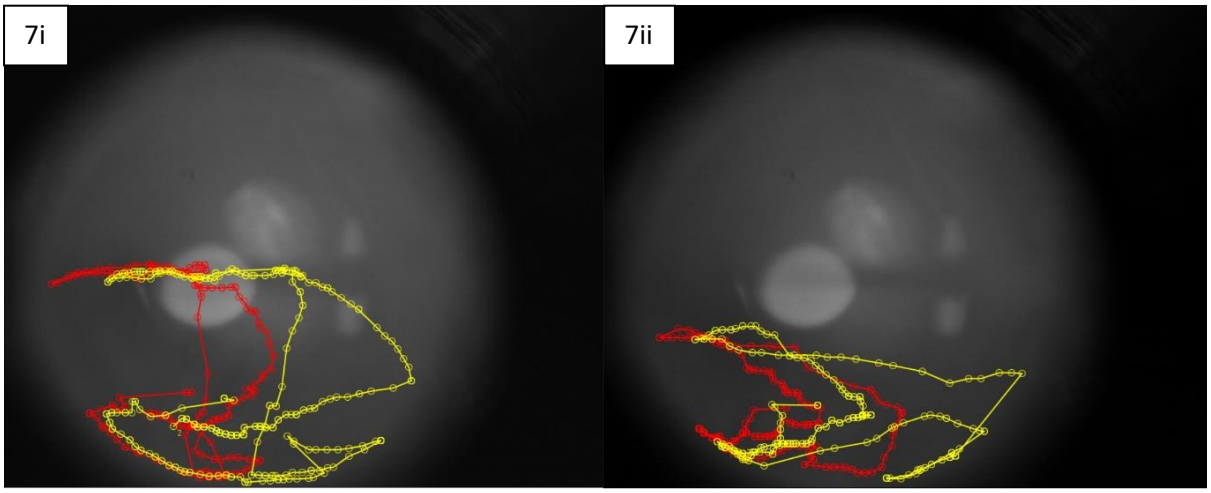
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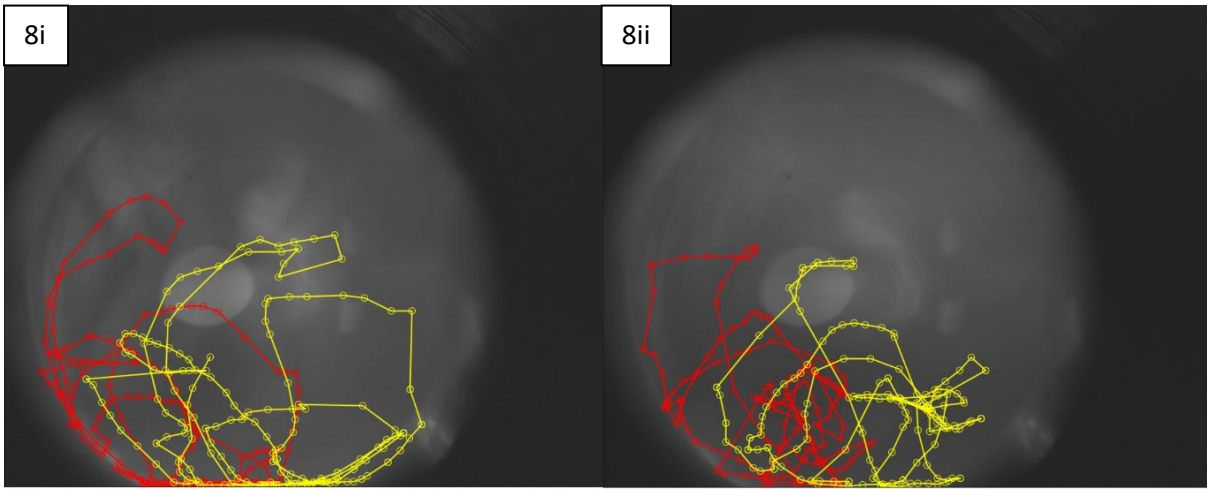
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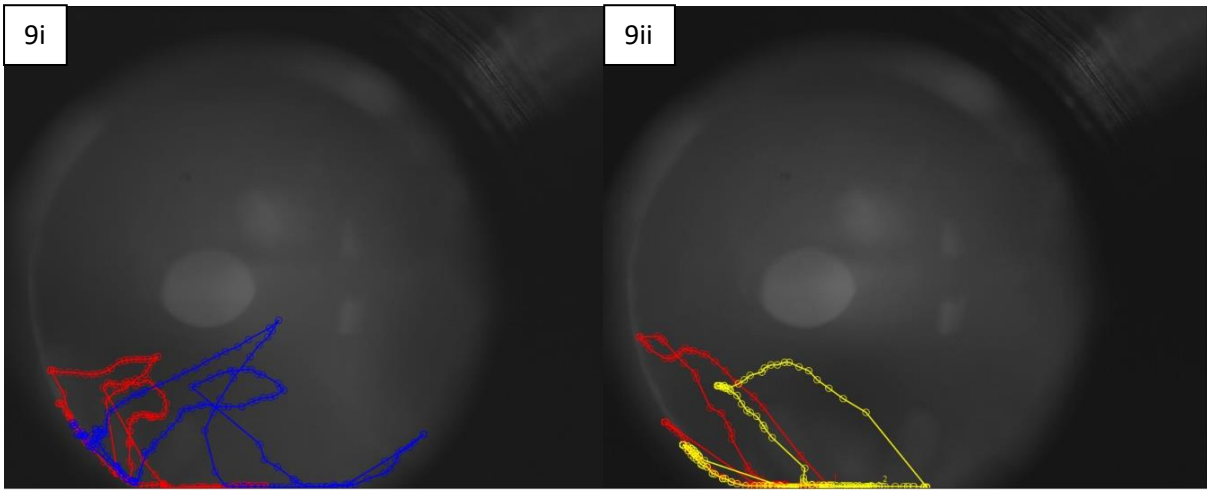
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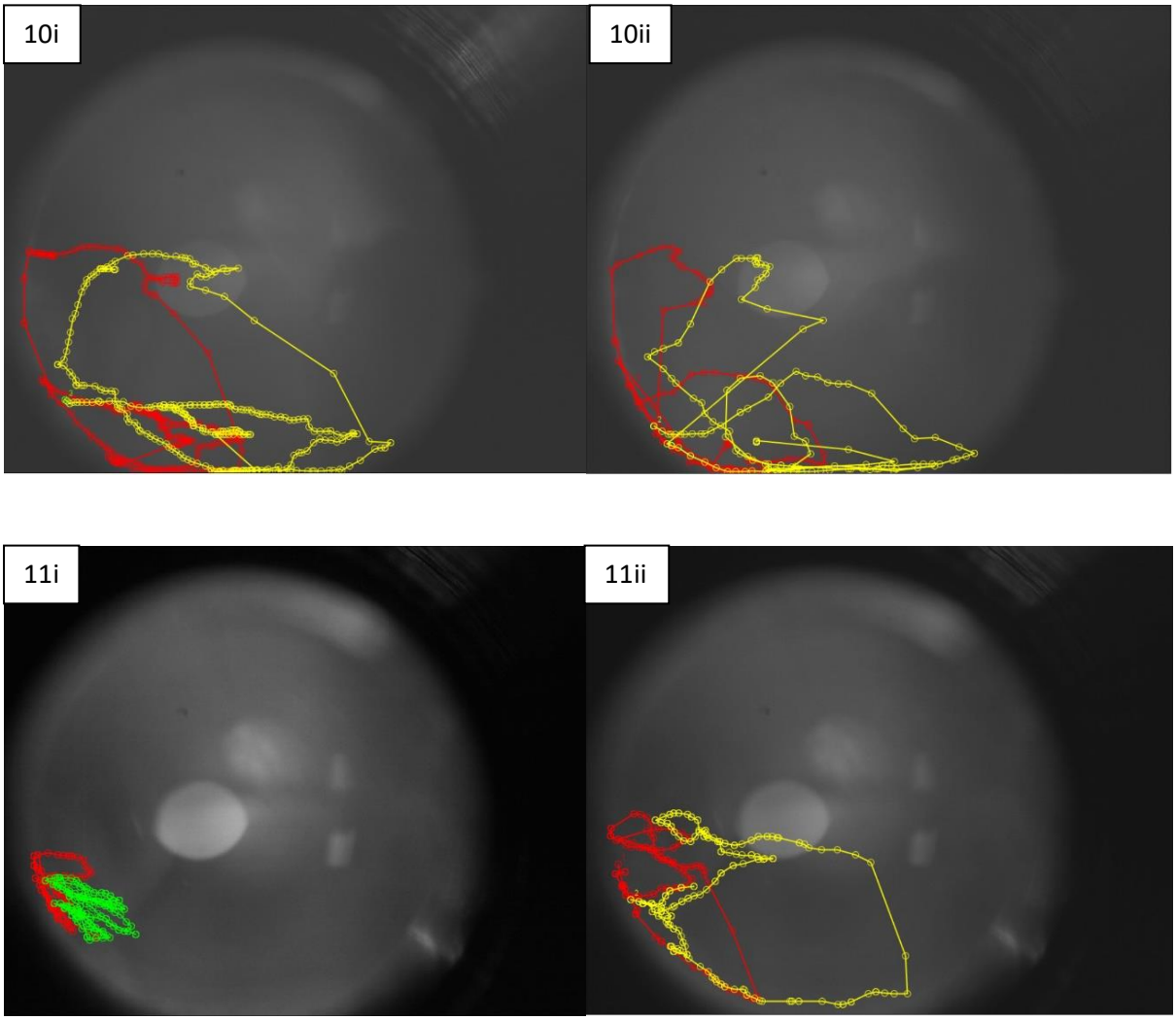
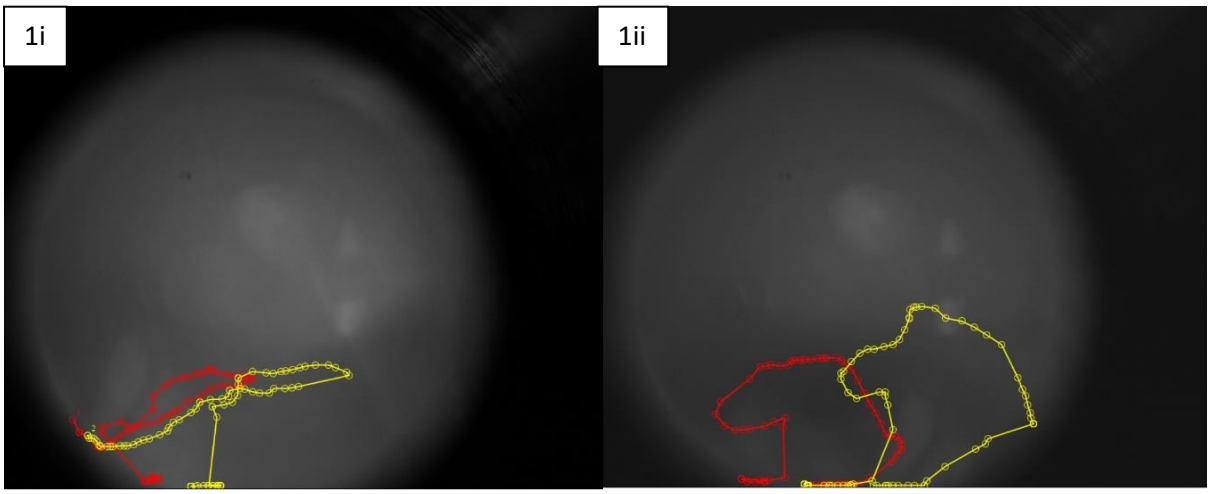
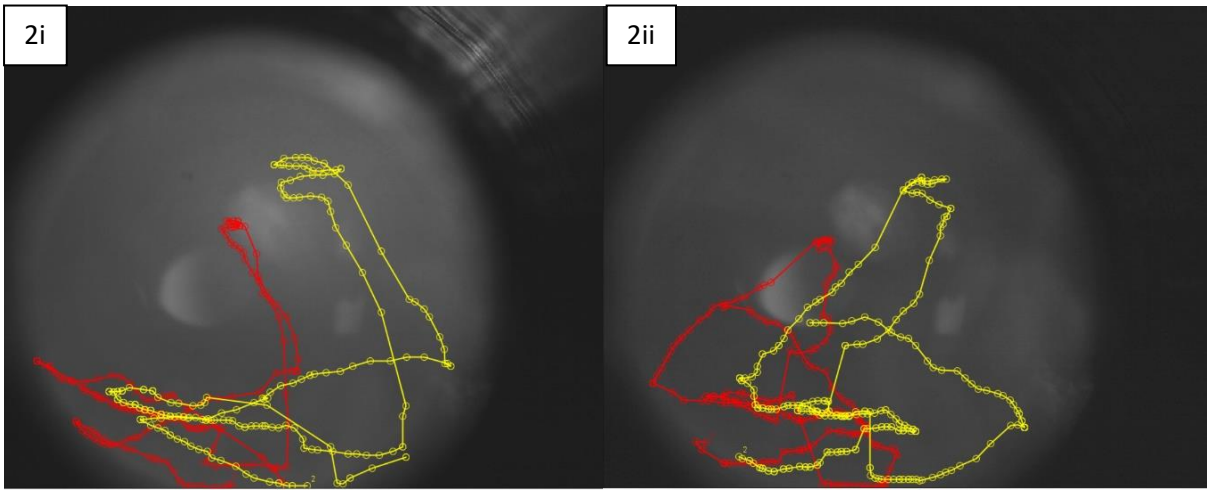
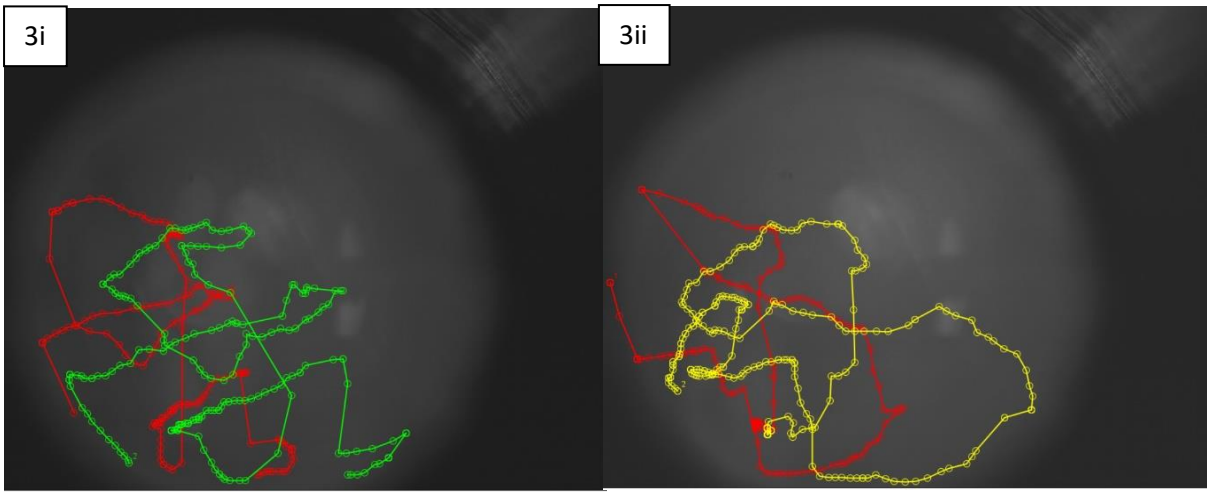


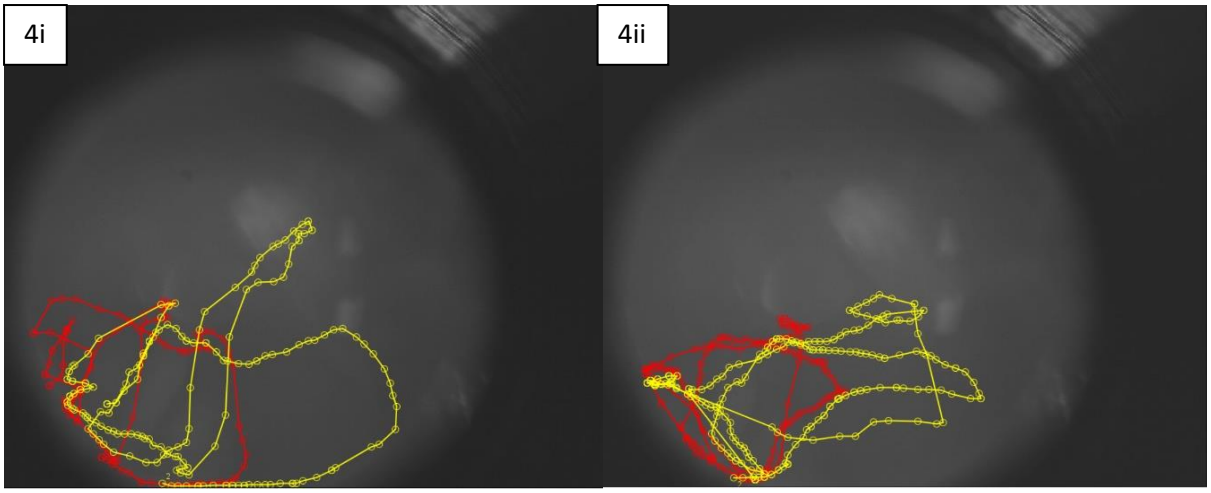
Figure 3. Raw tracks from the primary retina in response to the circle-bar delay priming paradigm. Each point refers to the centre of the retina. Red: Right retina. Yellow/Green/Blue: Left retina. Numbers 1-11 indicate the spider identification. i. Iteration 1. ii. Iteration 2.

Circle-Circle Tracks





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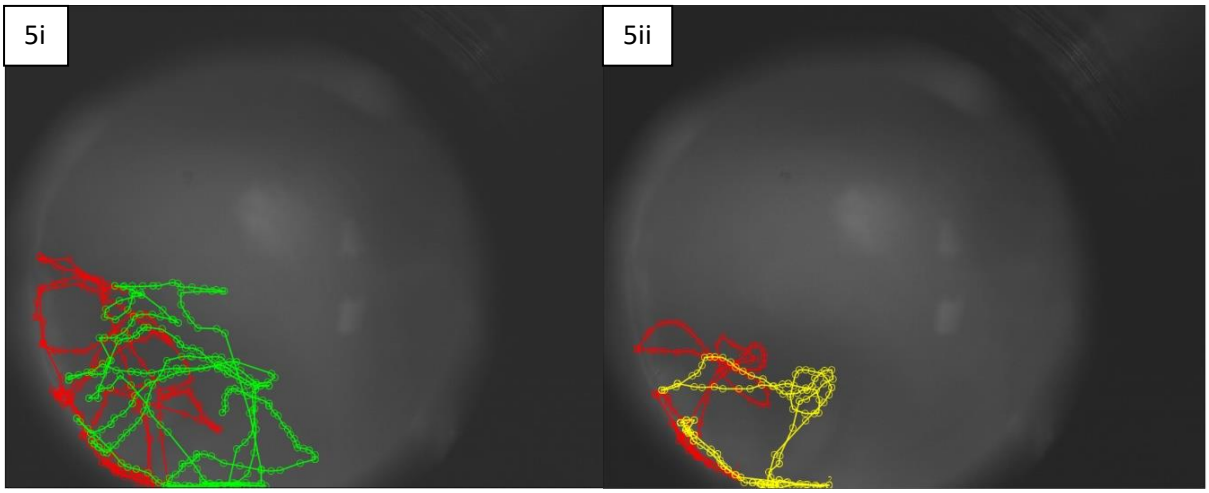
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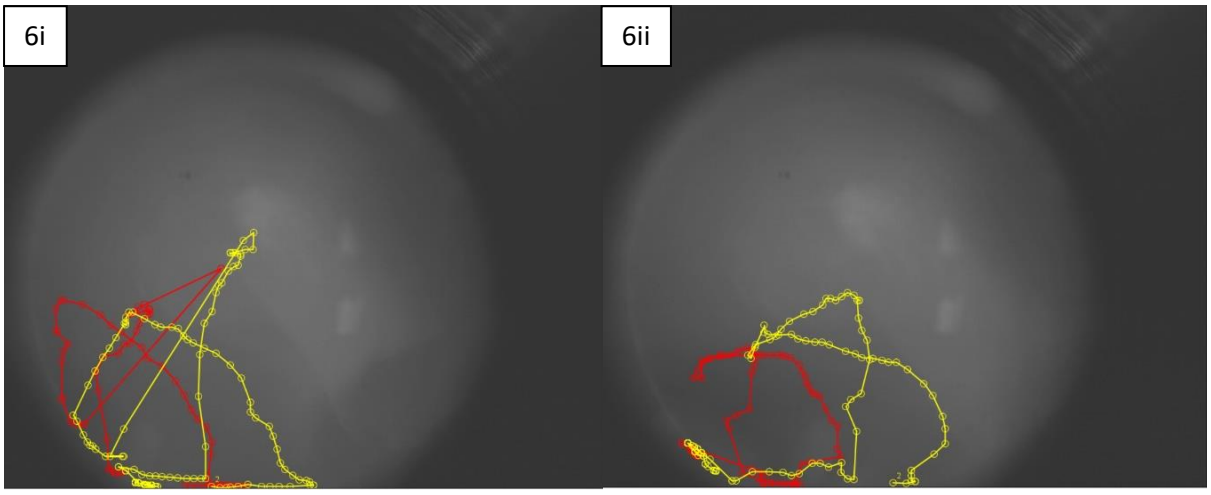
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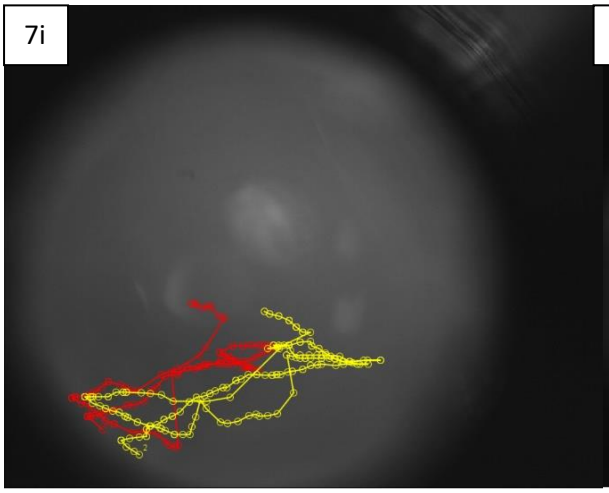

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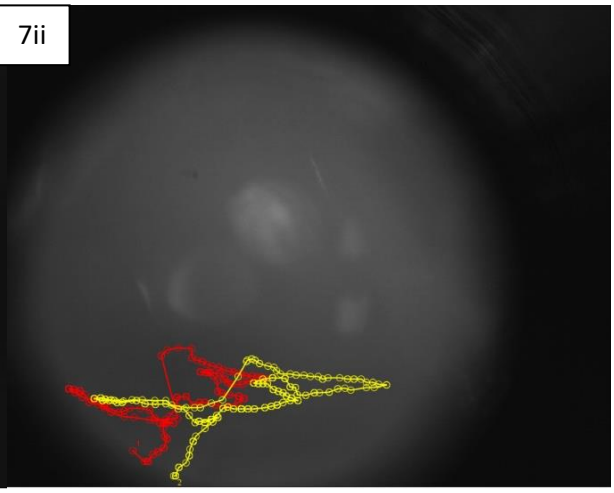

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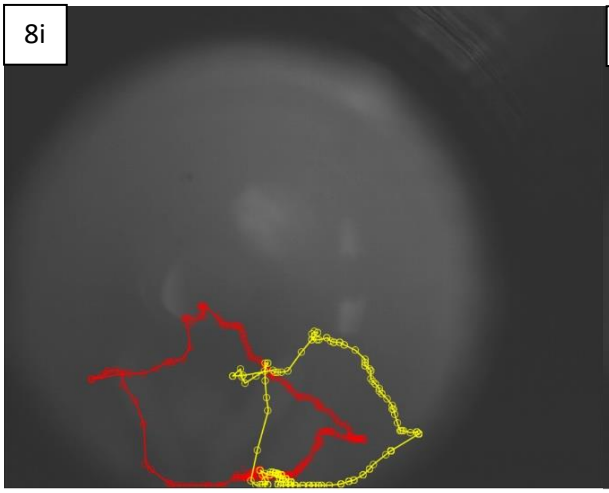

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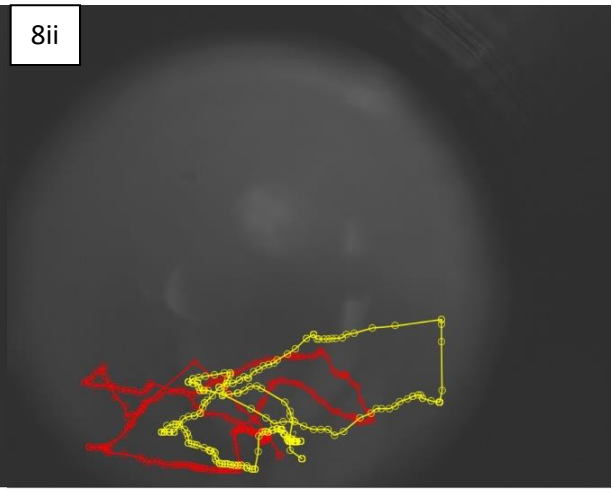

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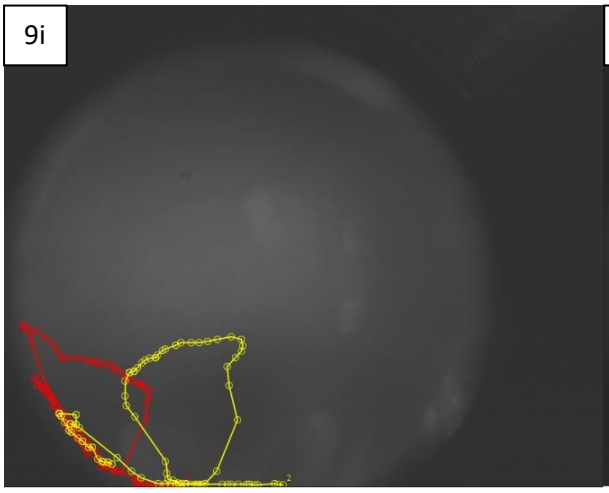

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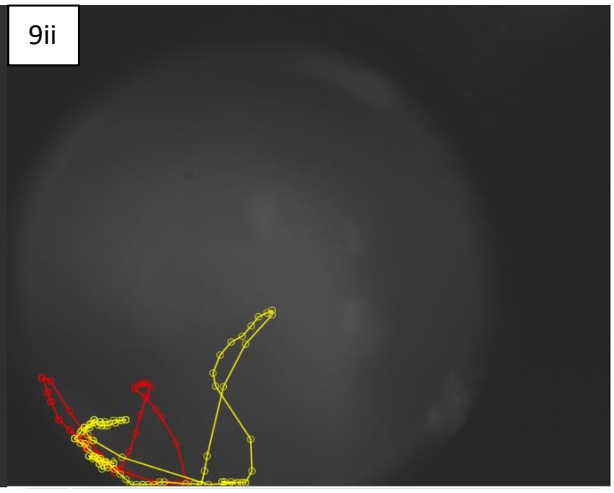


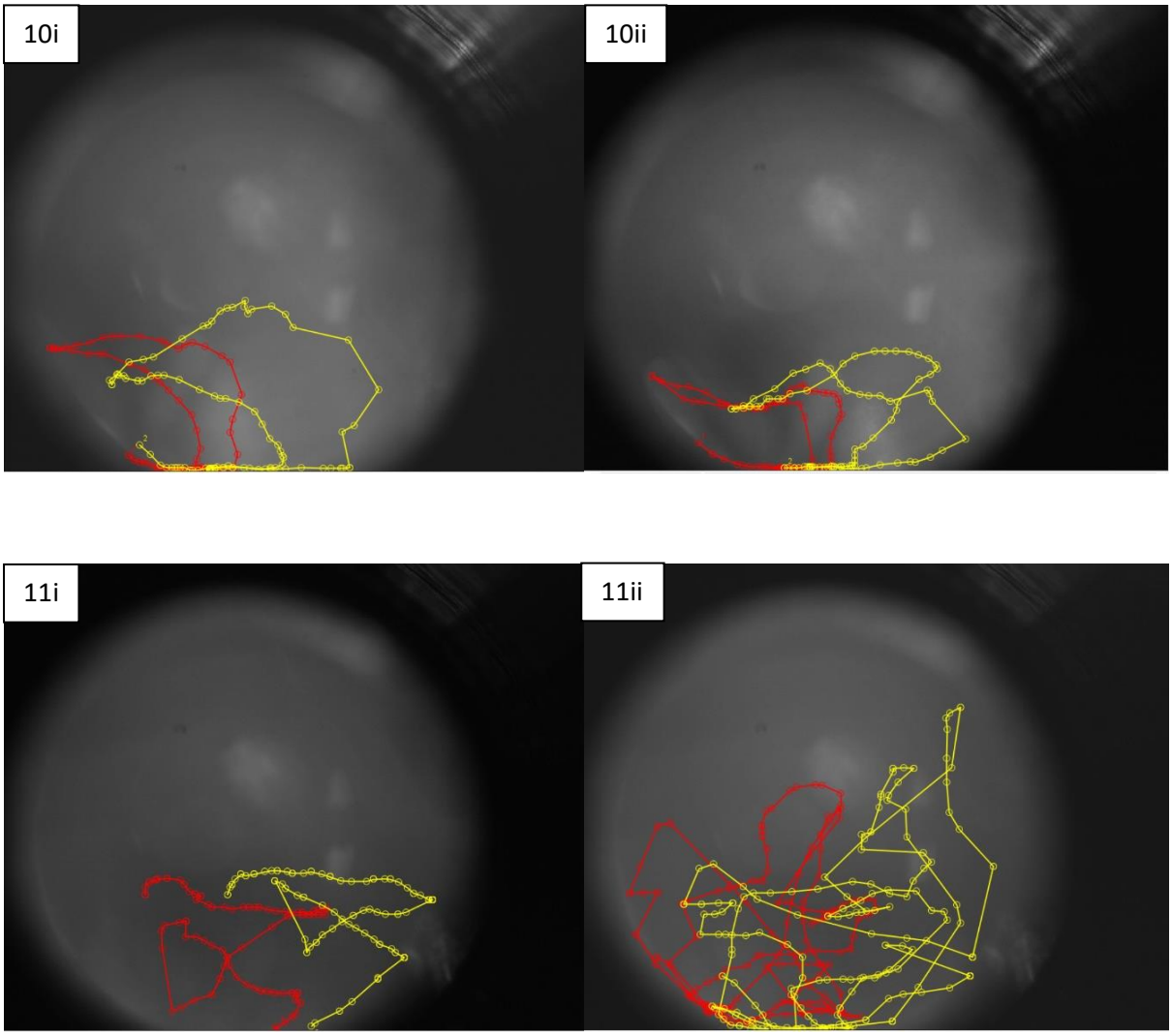
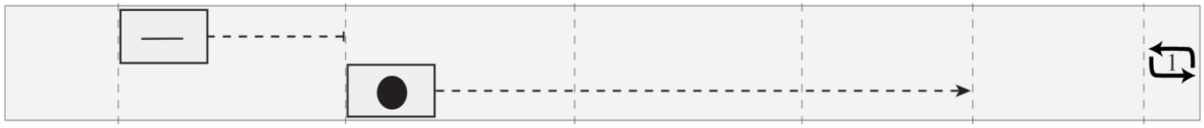
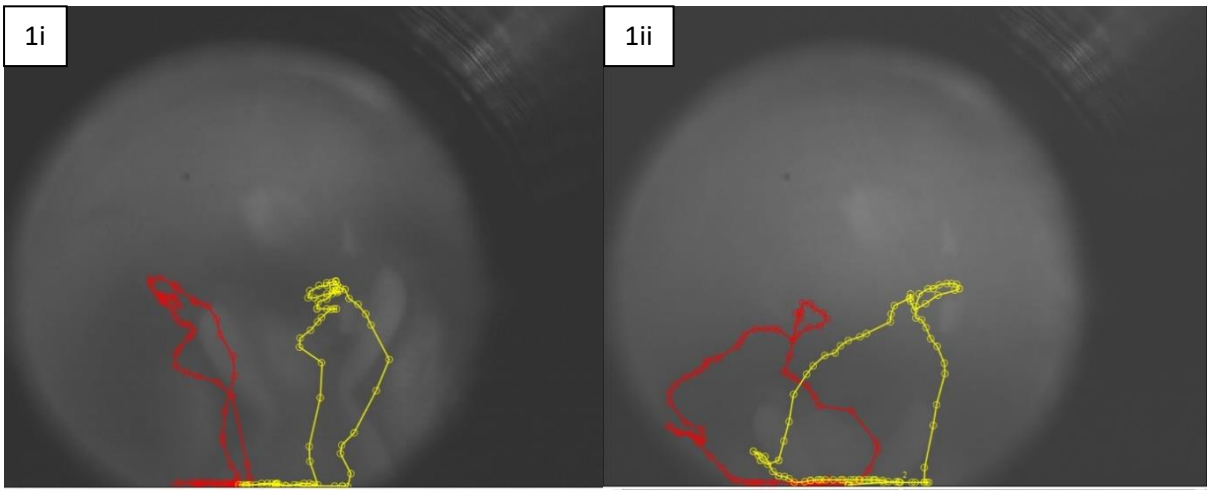
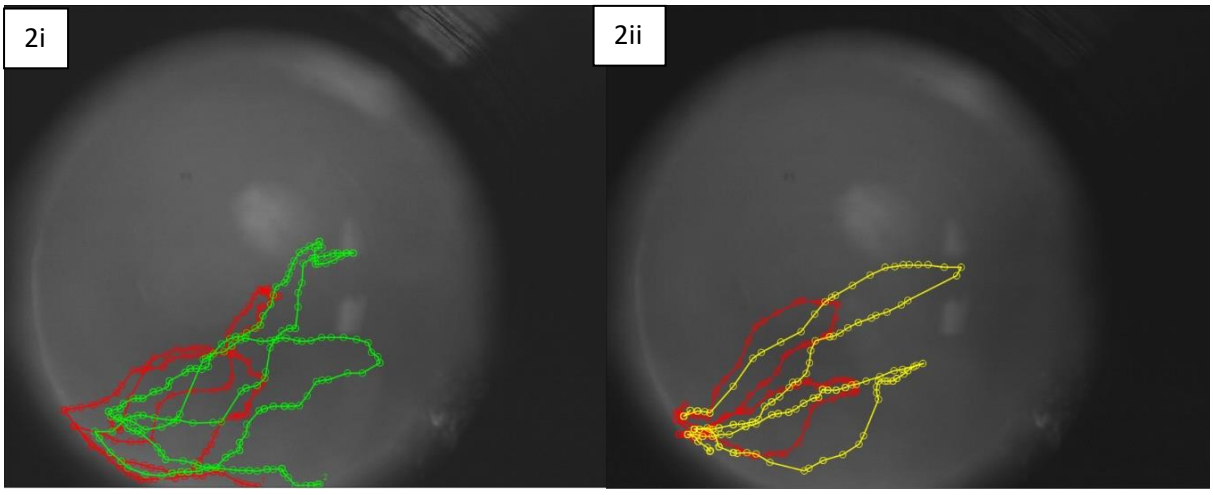


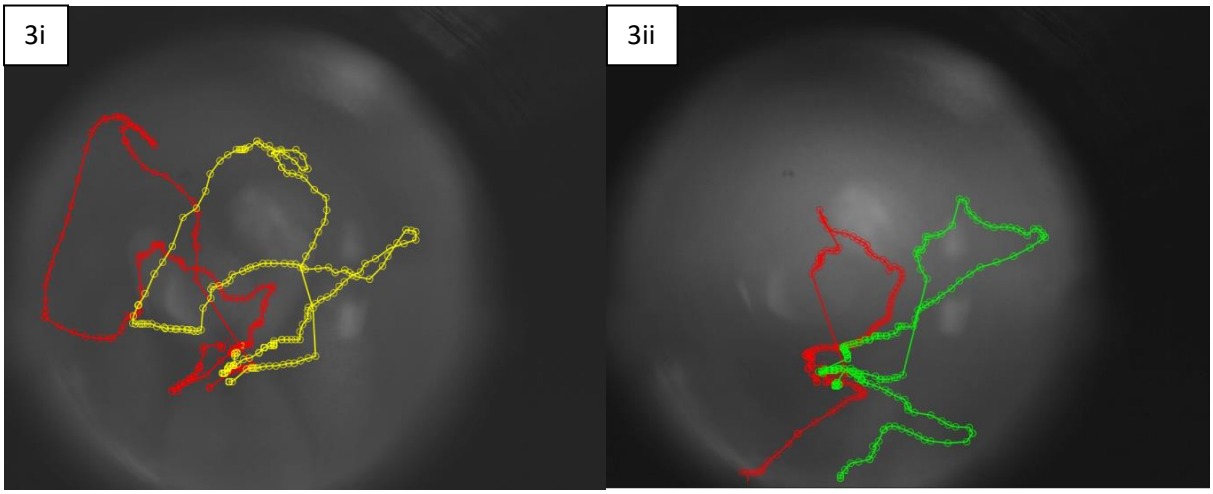
Figure 4. Raw tracks from the primary retina in response to the circle-circle priming paradigm. Each point refers to the centre of the retina. Red: Right retina. Yellow/Green: Left retina. Numbers 1-11 indicate the spider identification. i. Iteration 1. ii. Iteration 2.

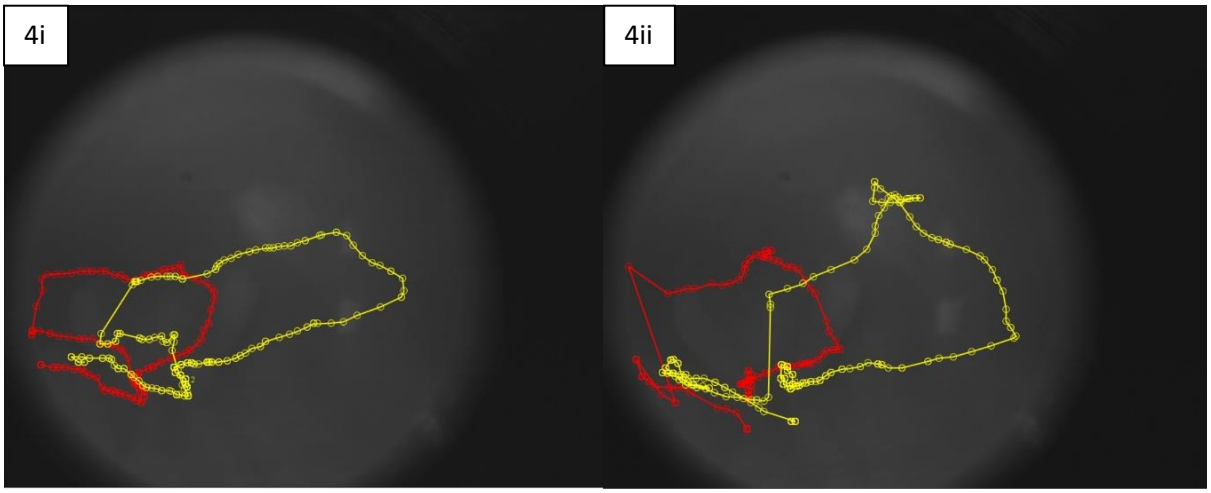
Bar-Circle Tracks







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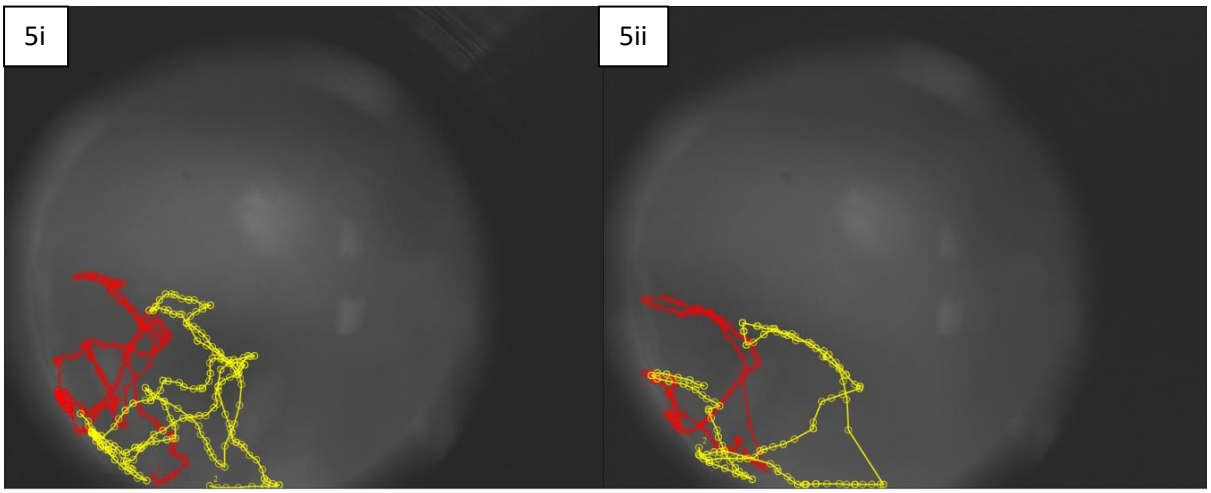
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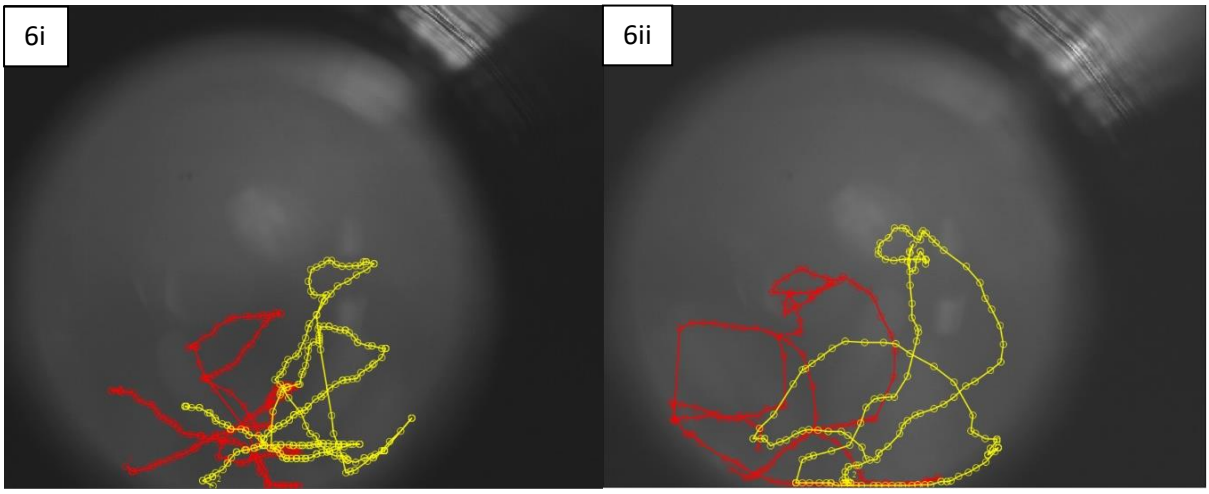
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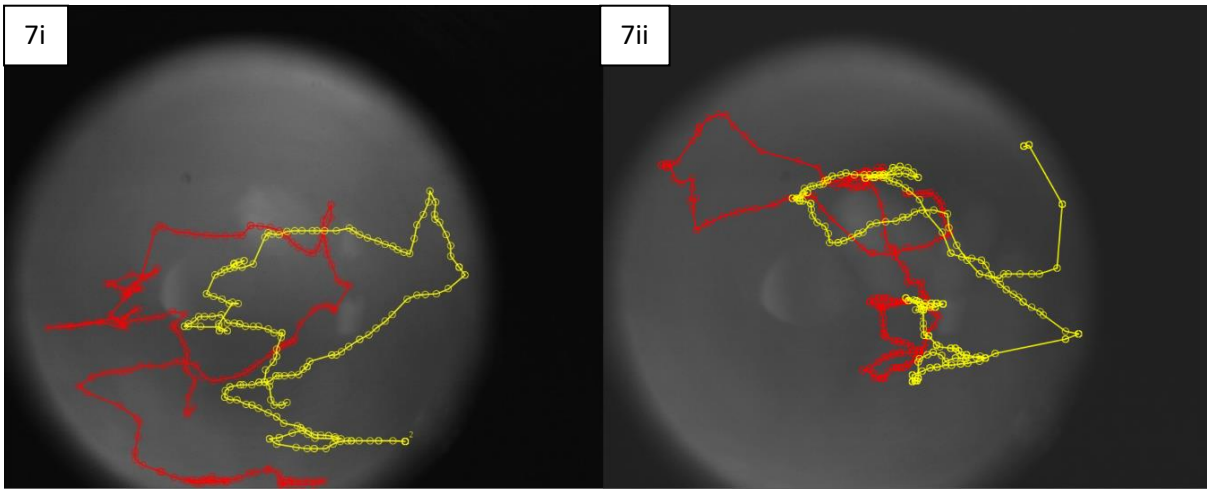
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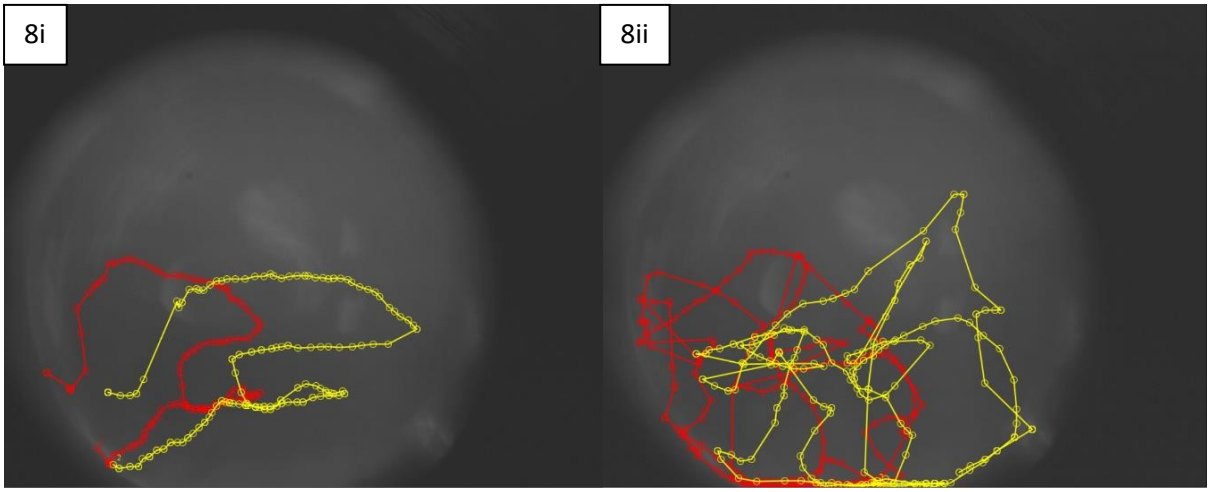
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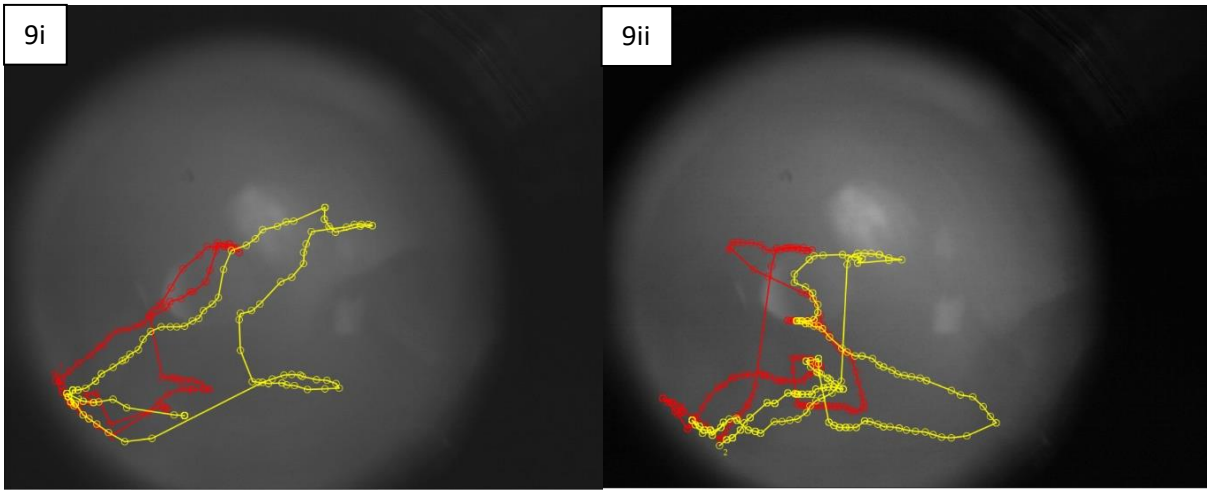
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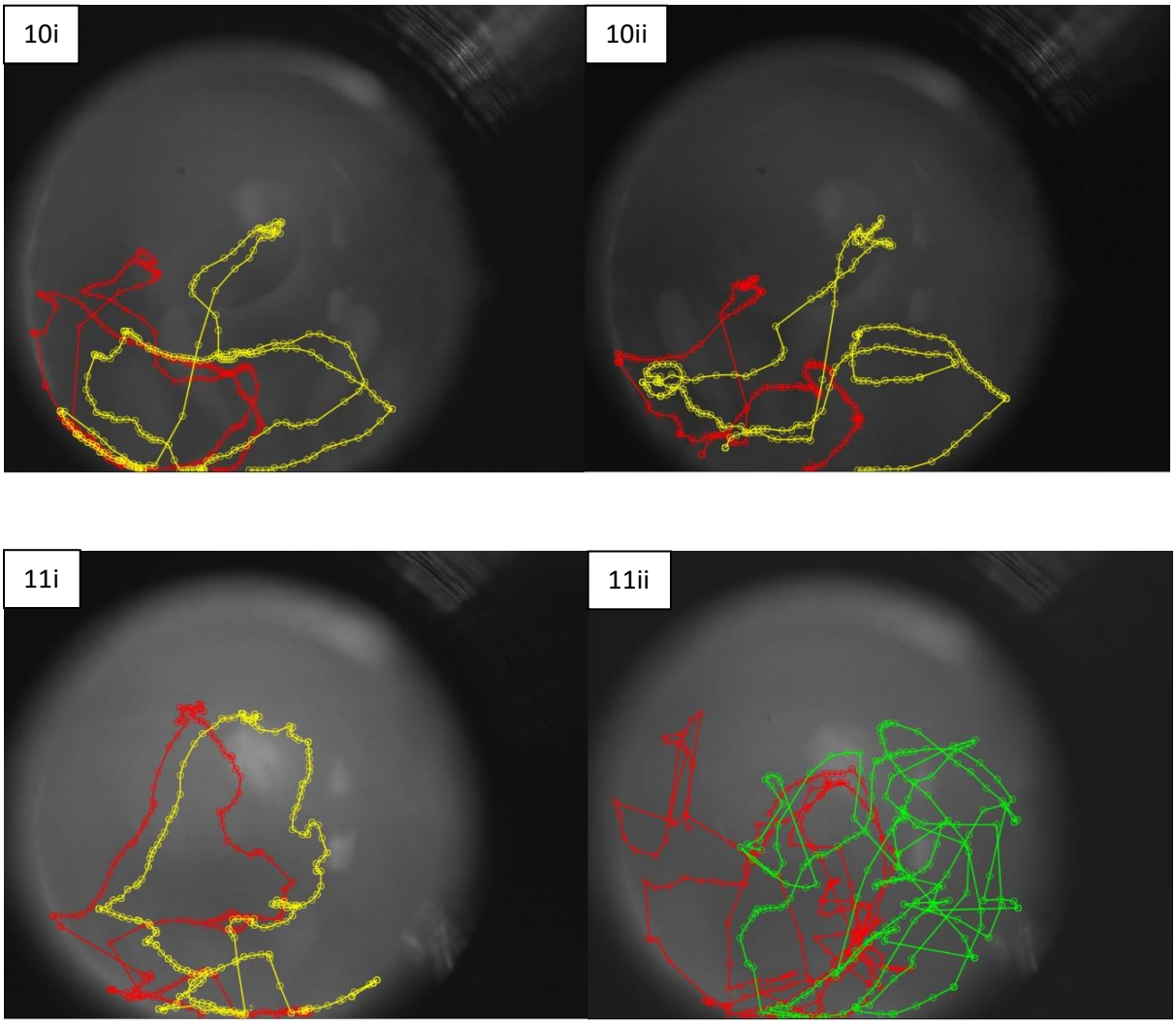
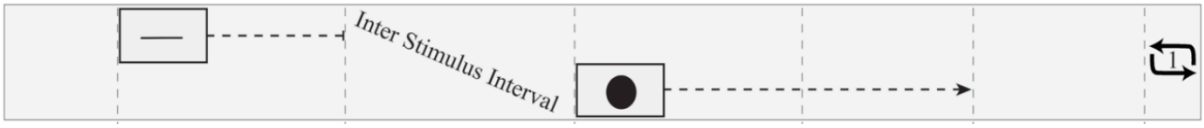
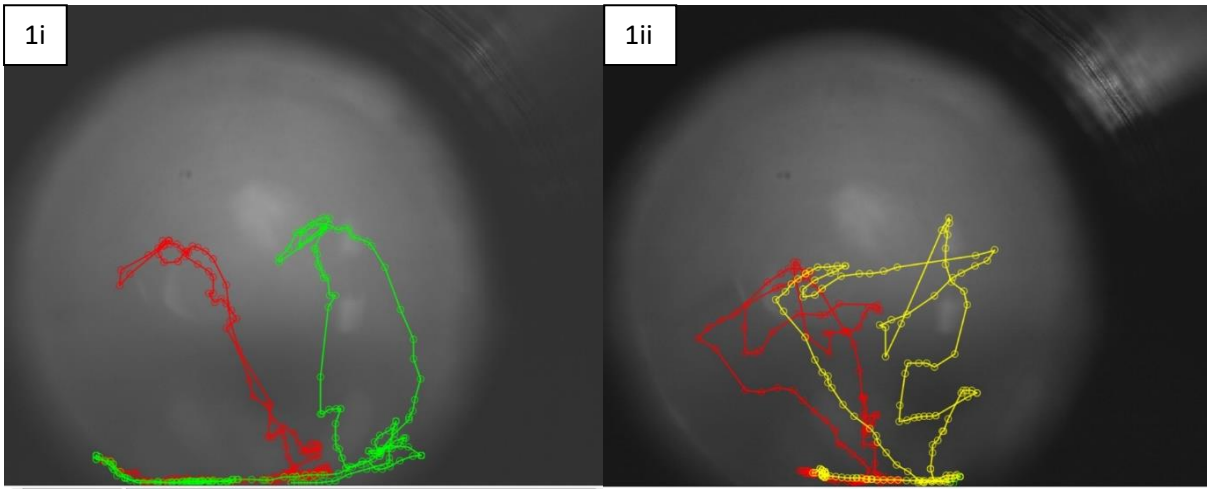
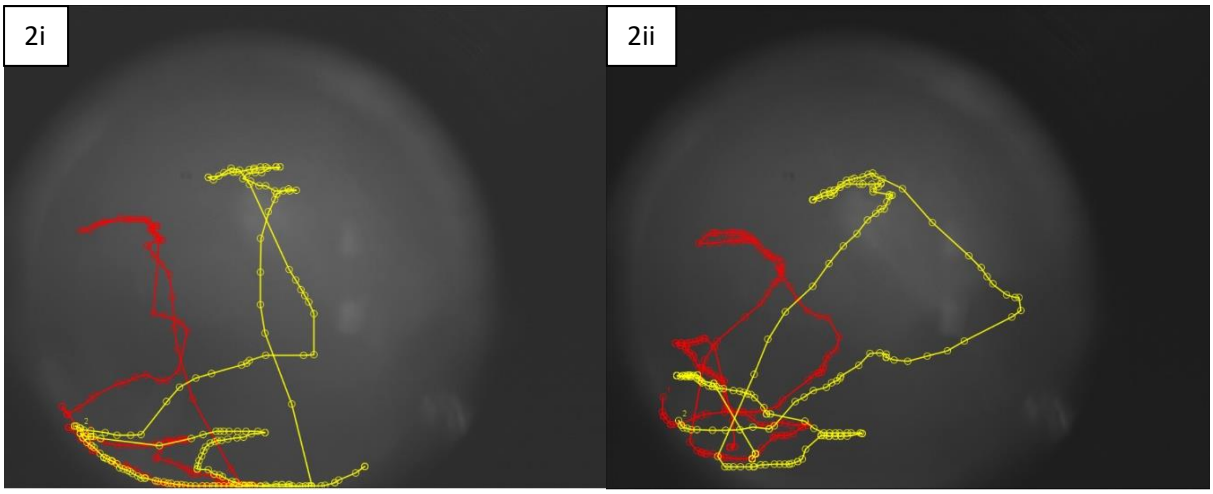


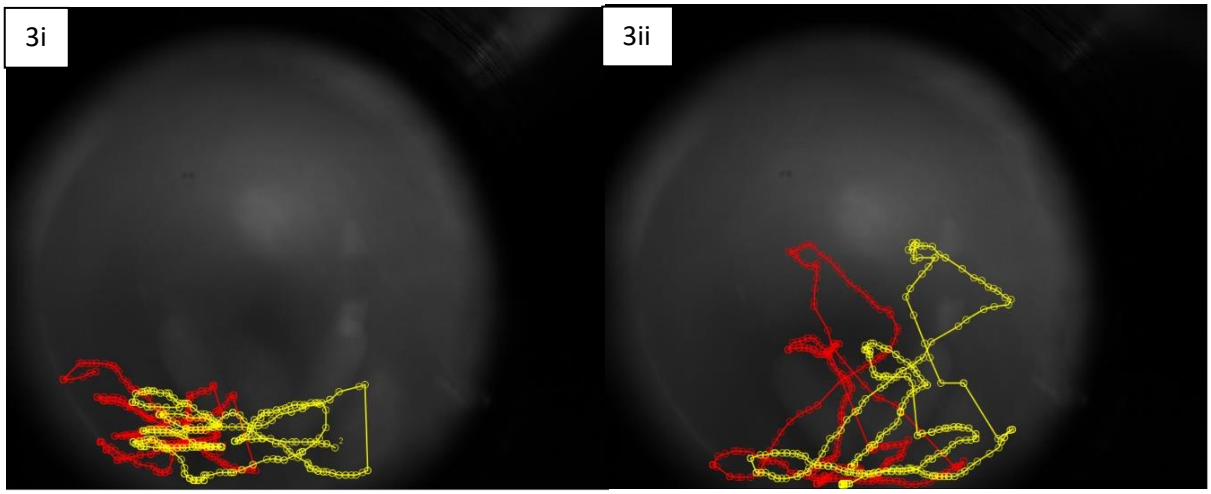
Figure 5. Raw tracks from the primary retina in response to the bar-circle priming paradigm. Each point refers to the centre of the retina. Red: Right retina. Yellow/Green: Left retina. Numbers 1-11 indicate the spider identification. i. Iteration 1. ii. Iteration 2.

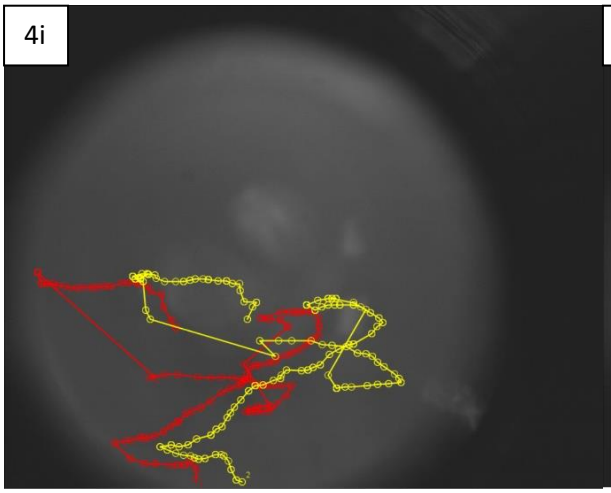
Bar-Circle Delay Tracks







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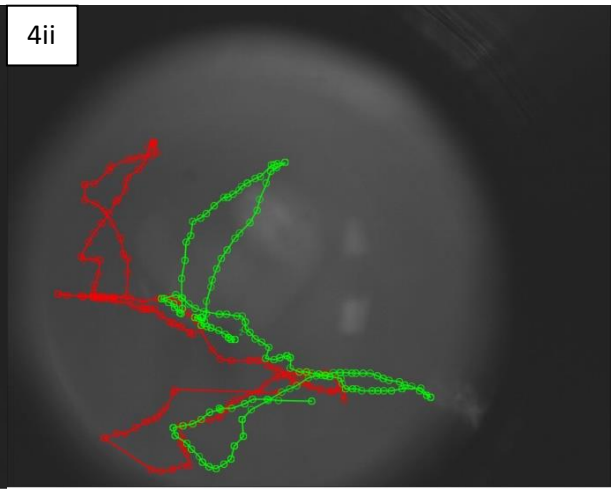
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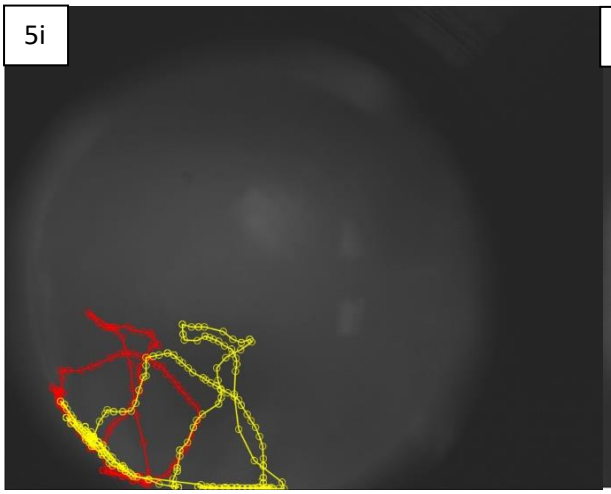
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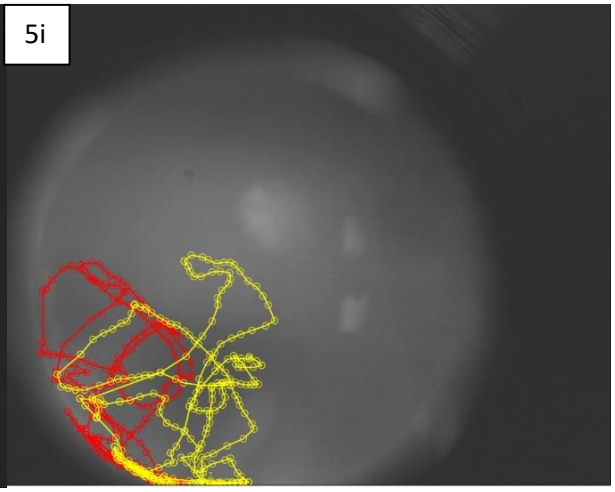
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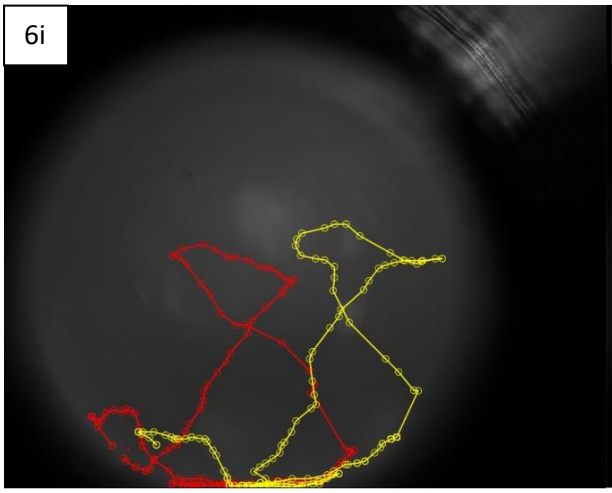
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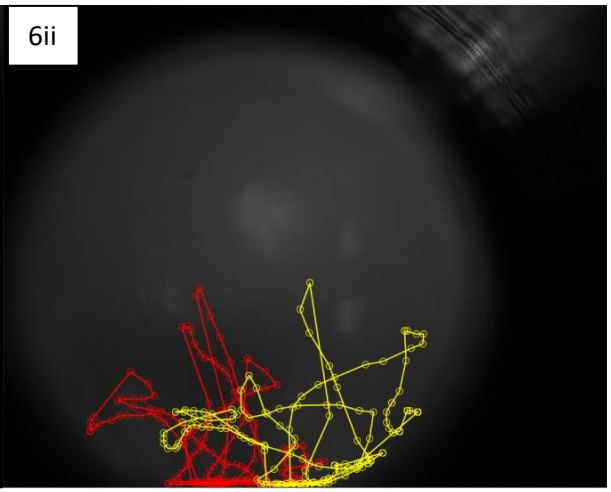
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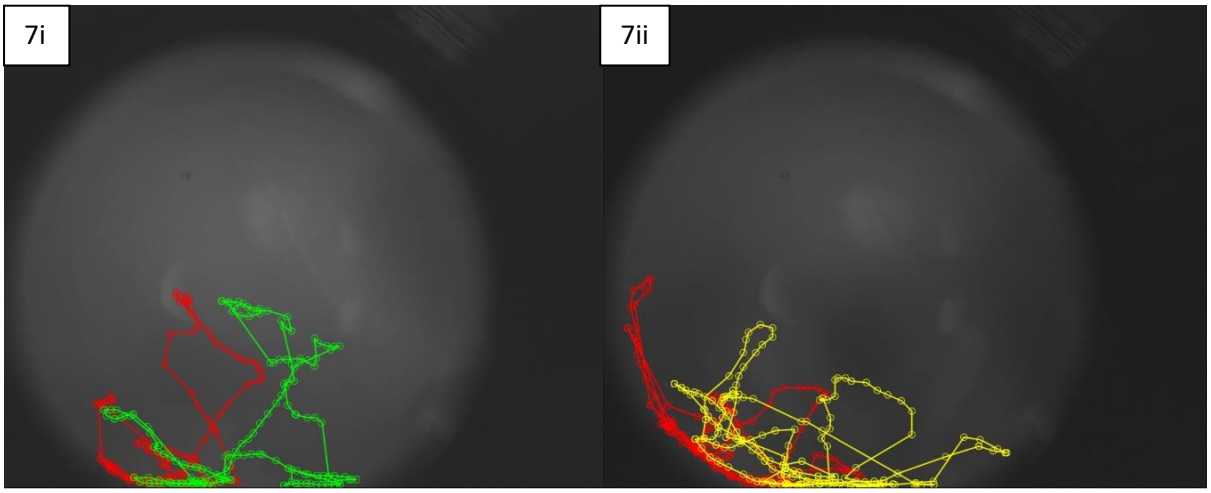
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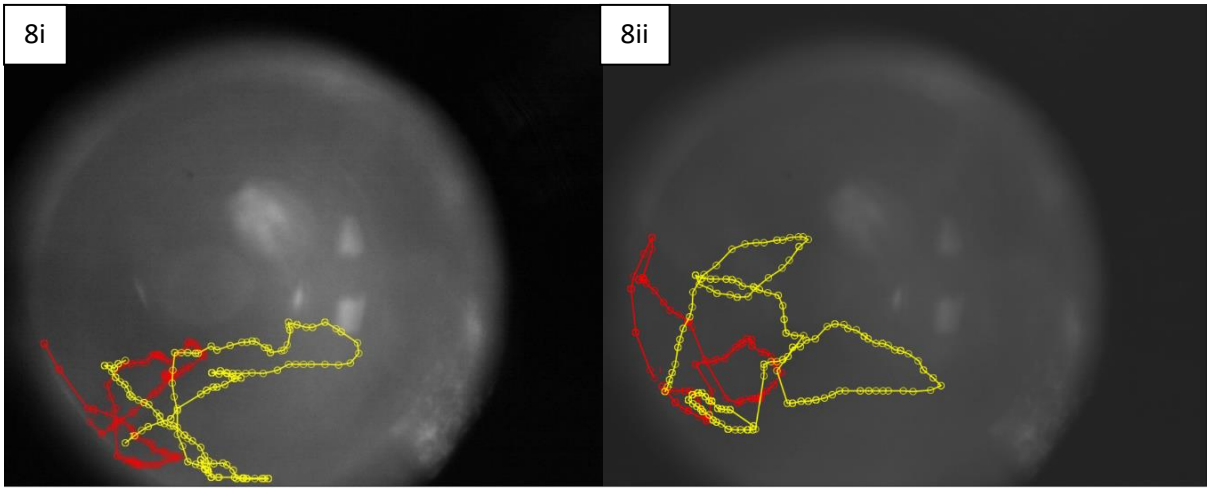
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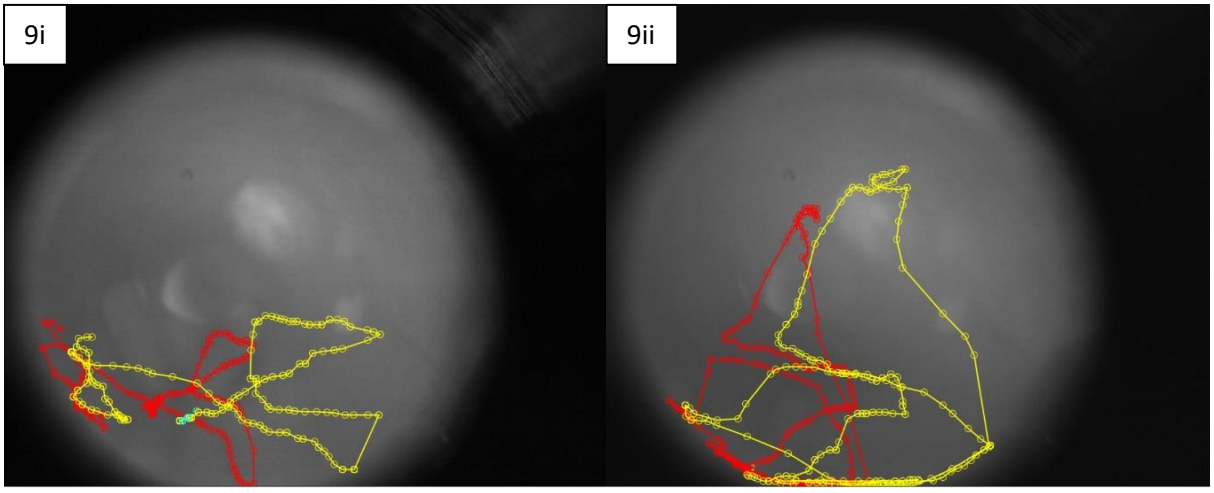
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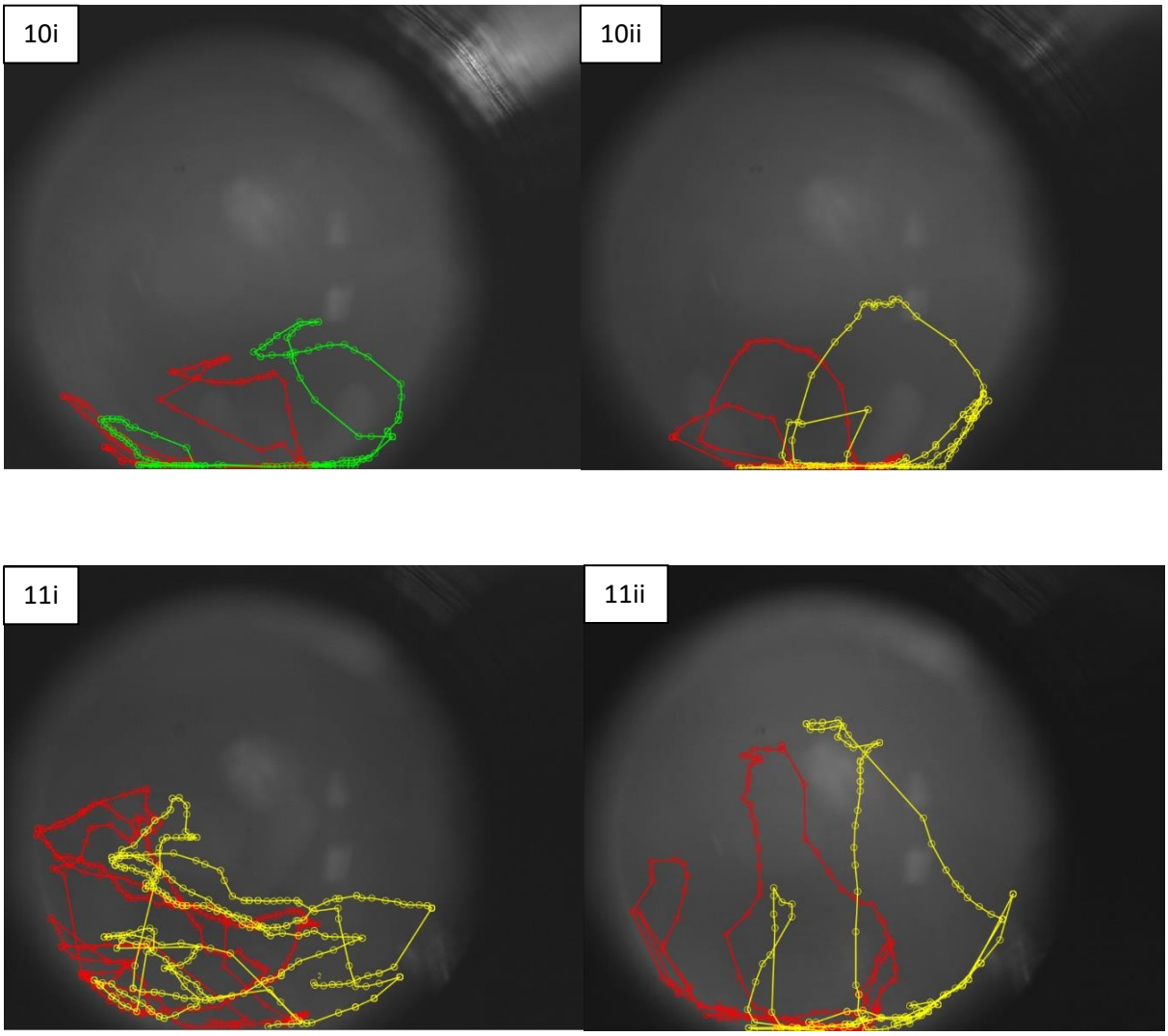
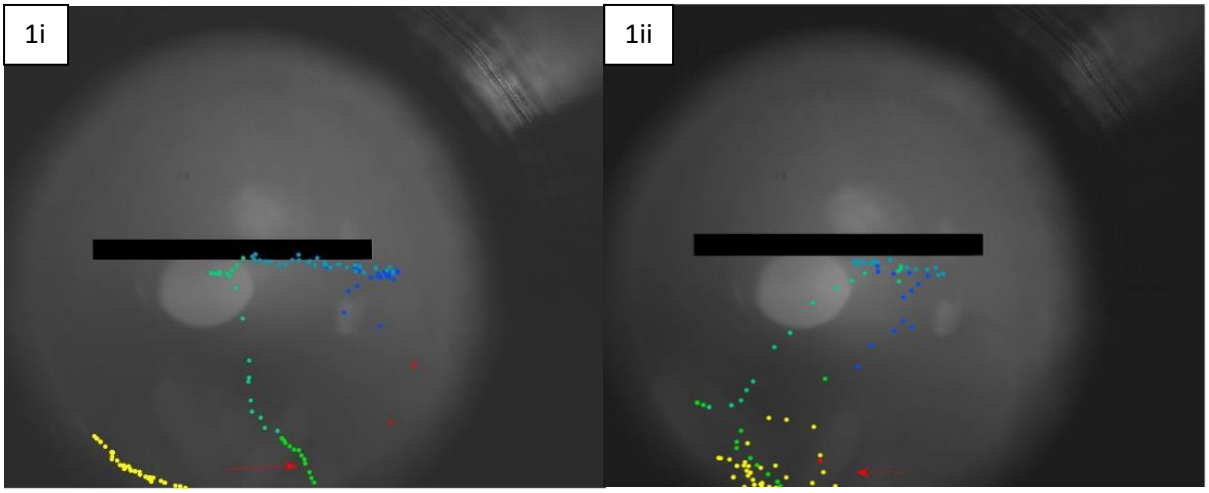
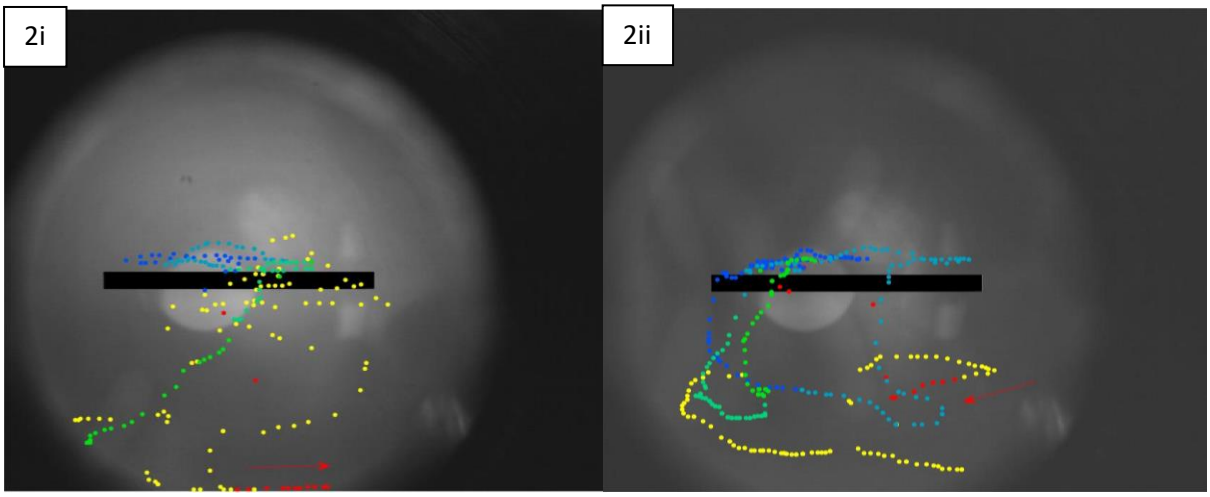
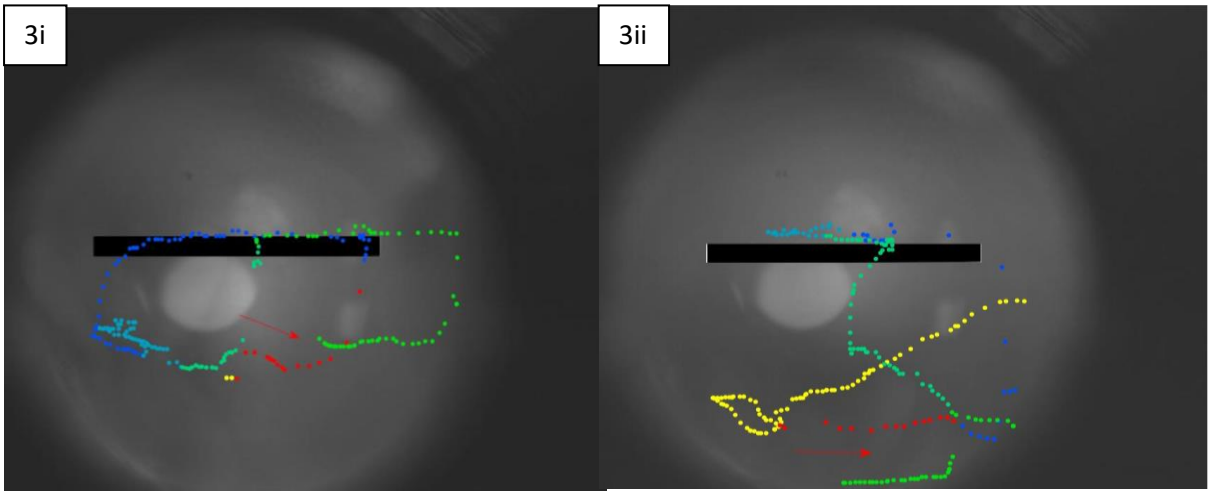


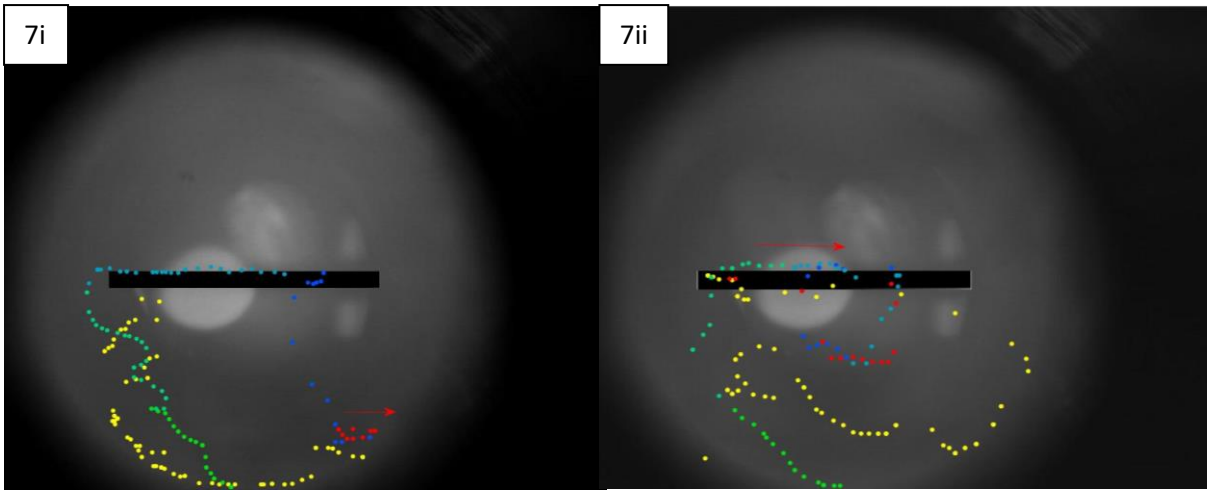
Figure 6. Raw tracks from the primary retina in response to the bar-circle delay priming paradigm. Each point refers to the centre of the retina. Red: Right retina. Yellow/Green: Left retina. Numbers 1-11 indicate the spider identification. i. Iteration 1. ii. Iteration 2.

Appendix 2.
Bar-Bar Tracks





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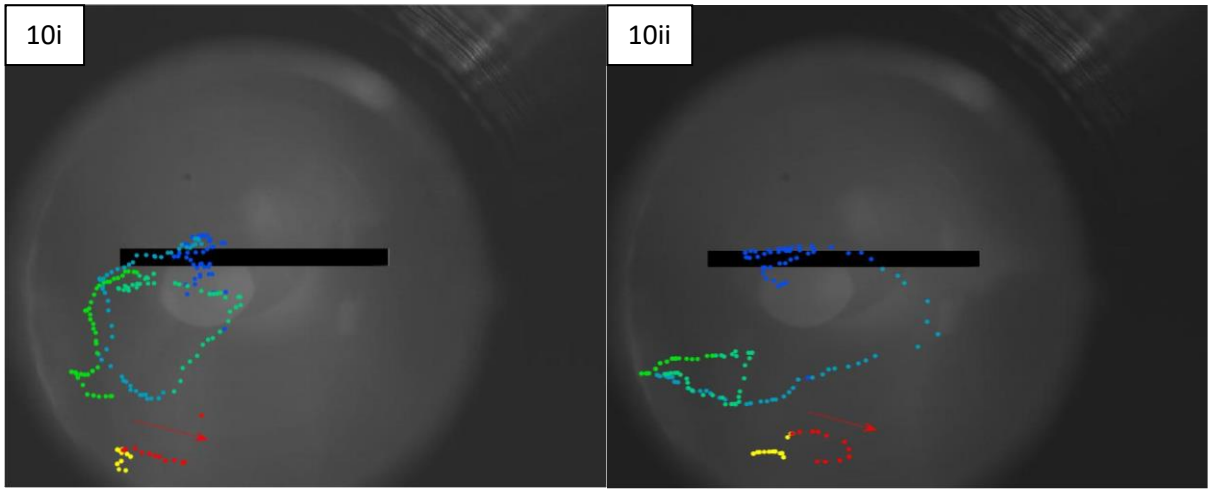
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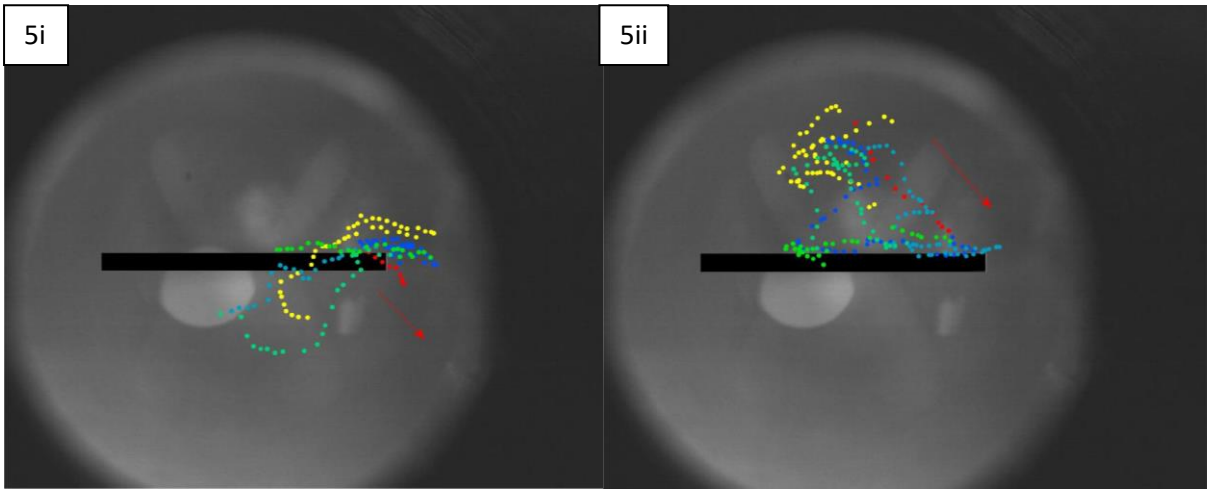
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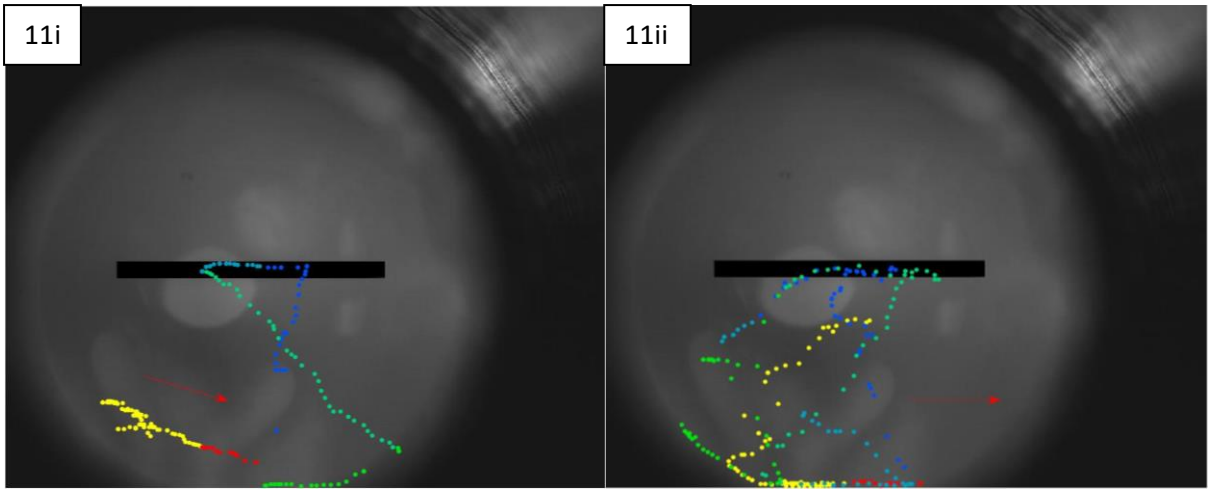
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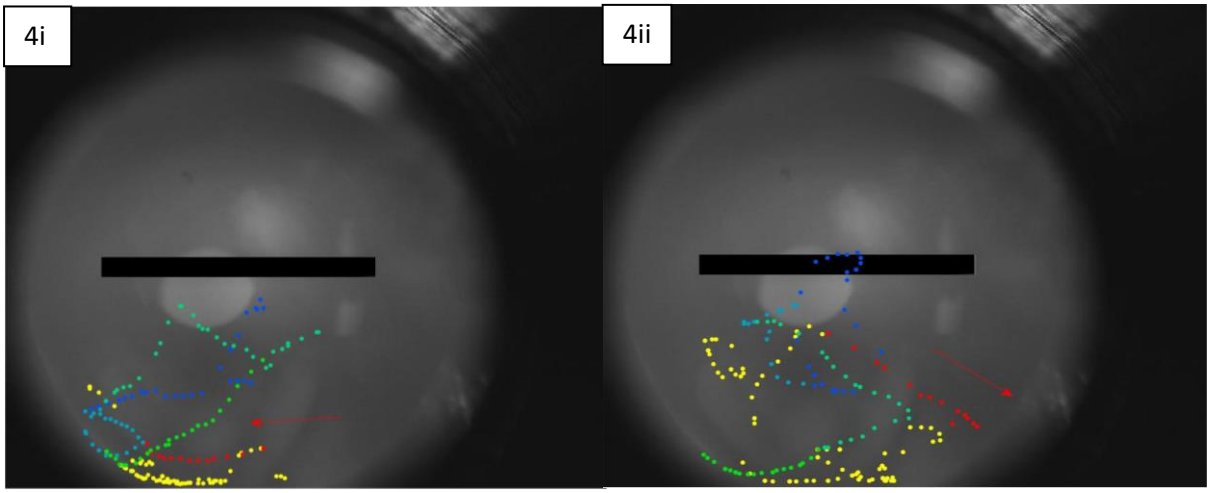
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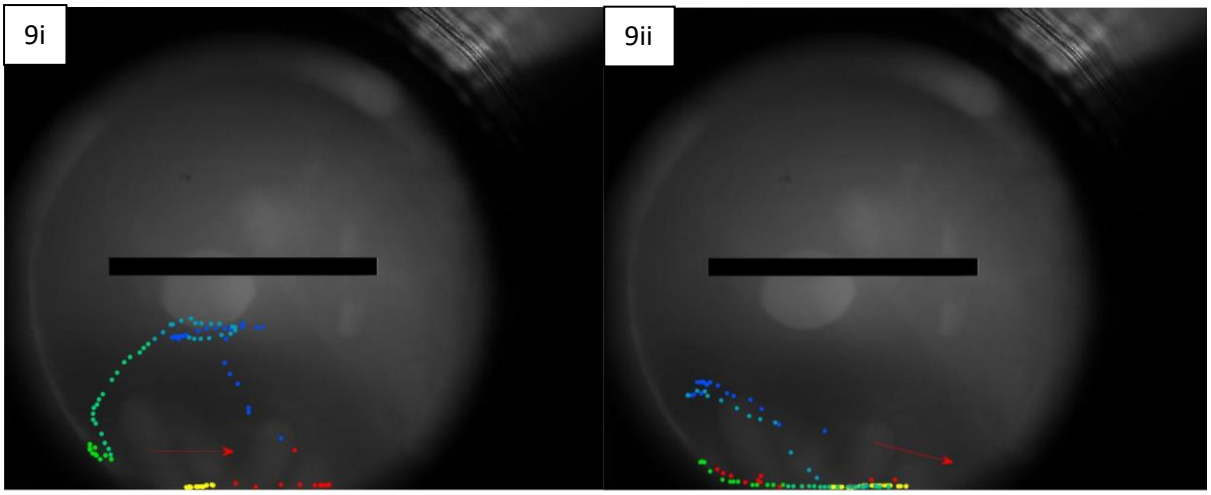
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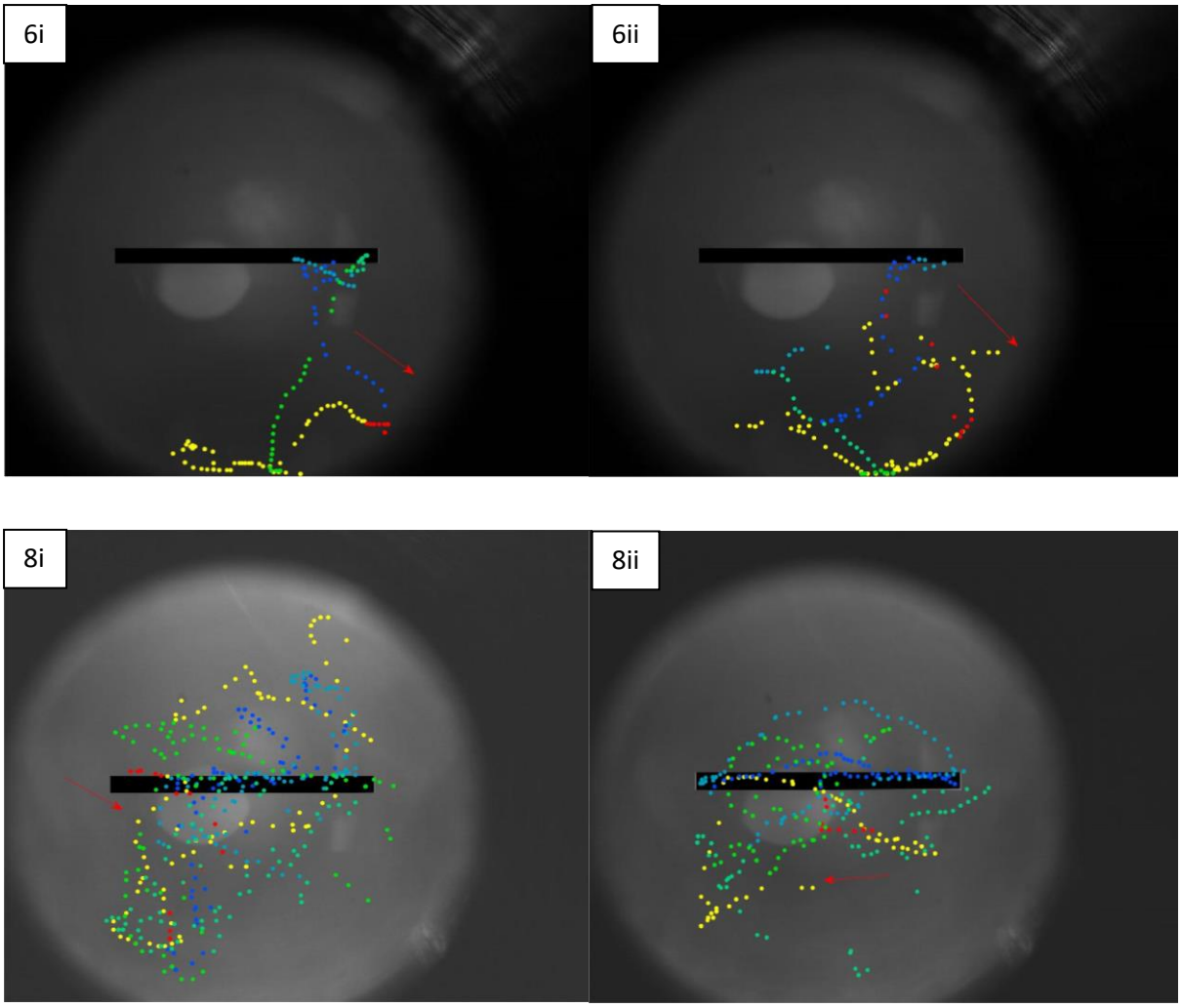
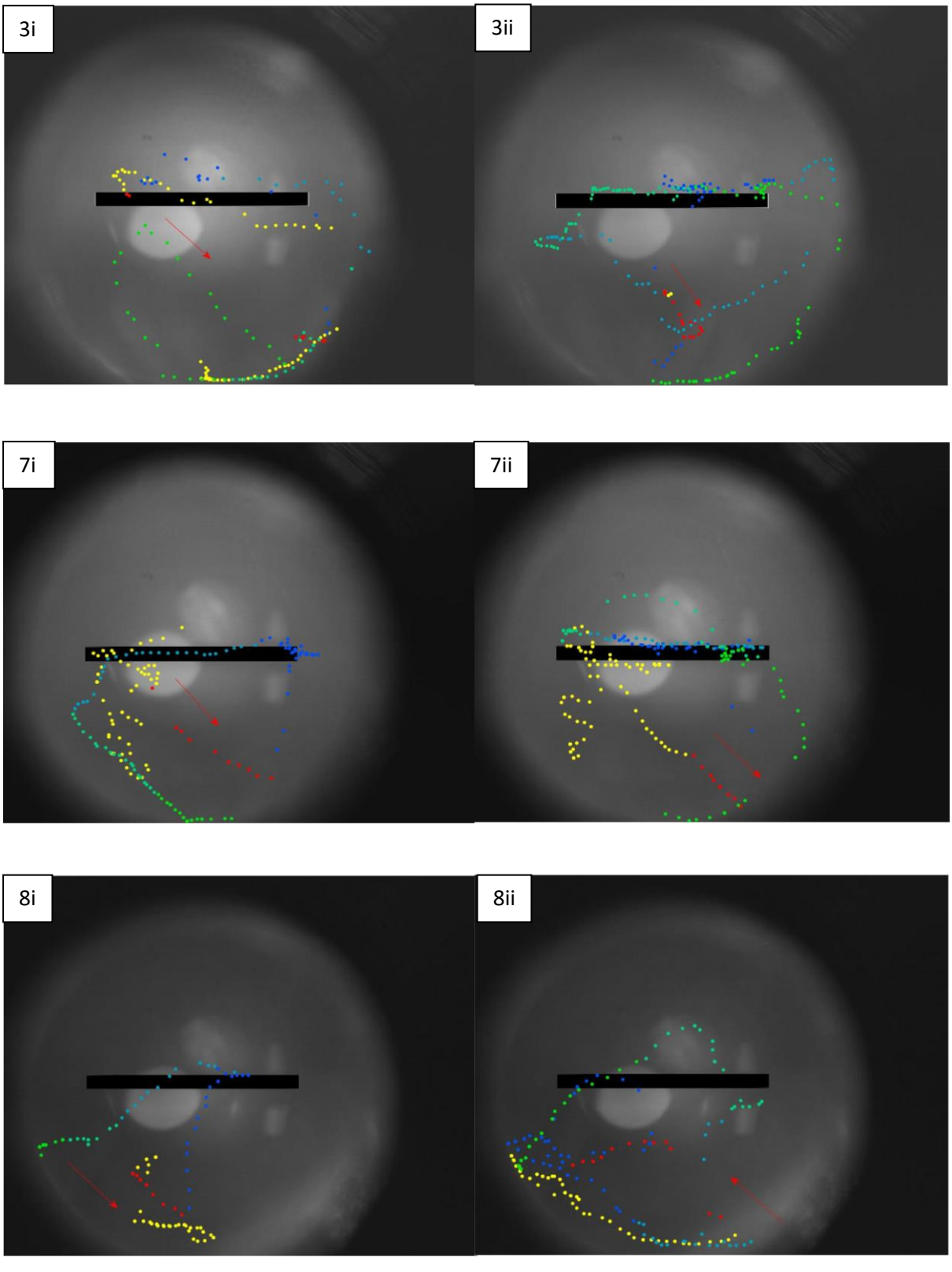
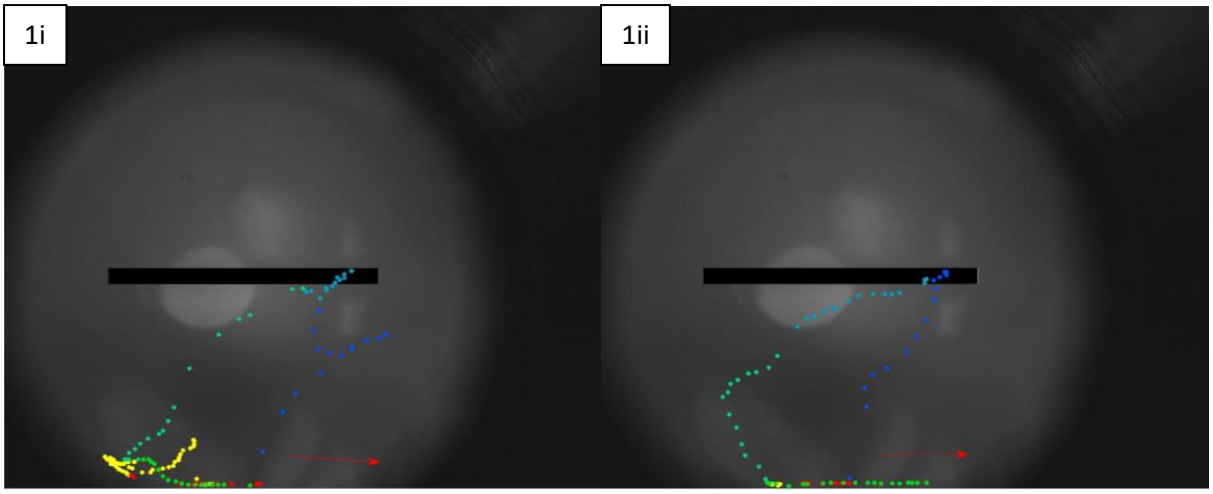


Figure 1. Track from the primary retina in response to the bar-bar priming paradigm. Only the track from the left retina is shown. Each point refers to the centre of the retina. Yellow: spontaneous activity, prior to presentation of stimuli. Red: Movement during the priming stimulus; Red arrow shows the initial direction of the saccade. Blue to green: pattern of scanning during the presentation of the main stimulus. Main stimulus is superimposed onto the image for reference. Tracks are ordered in clarity, from the most targeted tracks to the least targeted. Numbers 1-11 indicate the spider identification number. i. Iteration 1. ii. Iteration 2.

Circle-Bar Tracks

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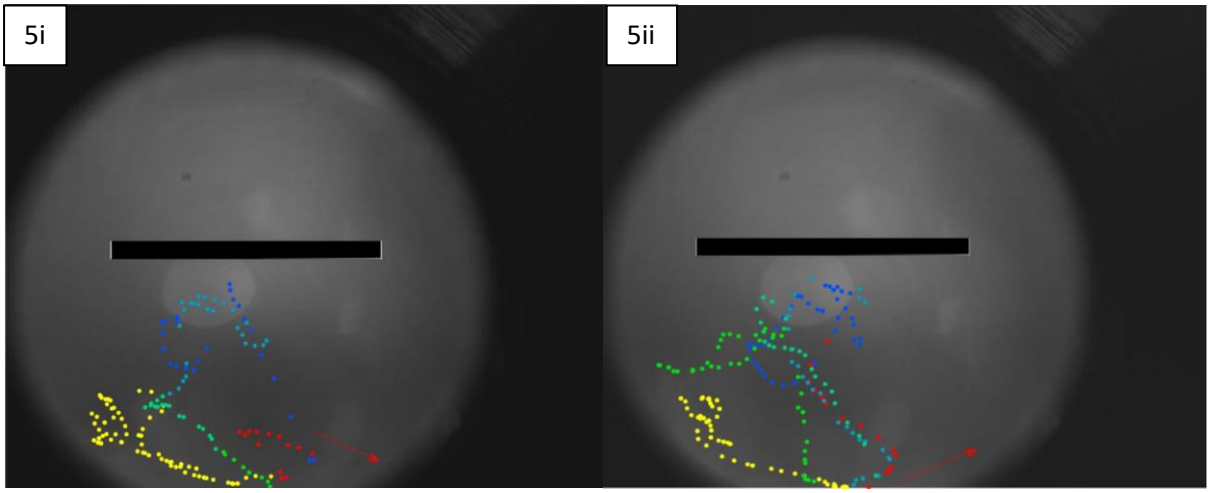
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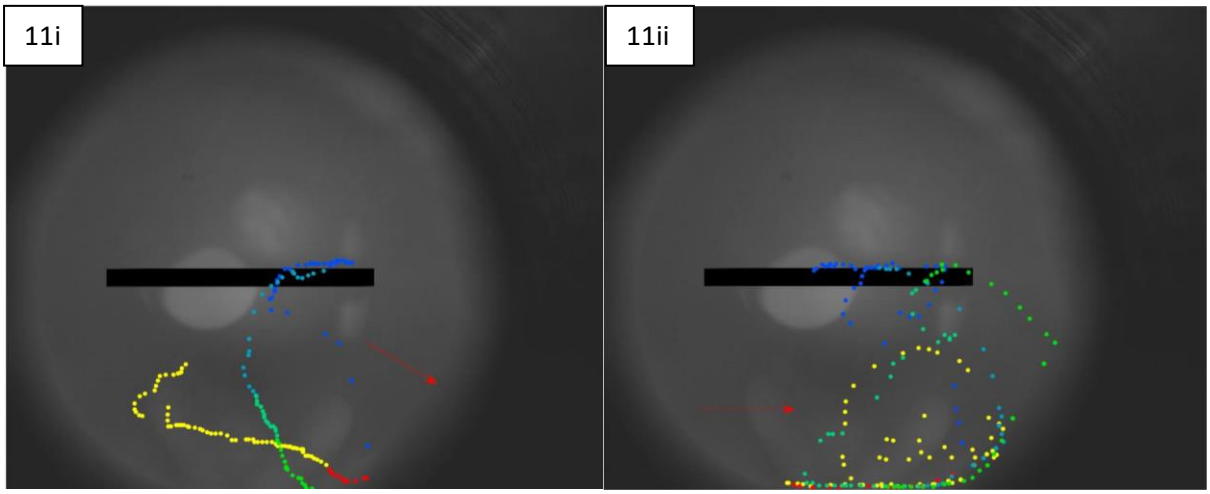
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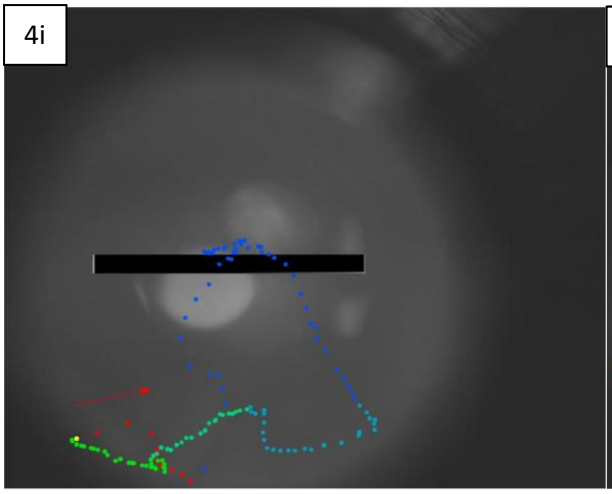
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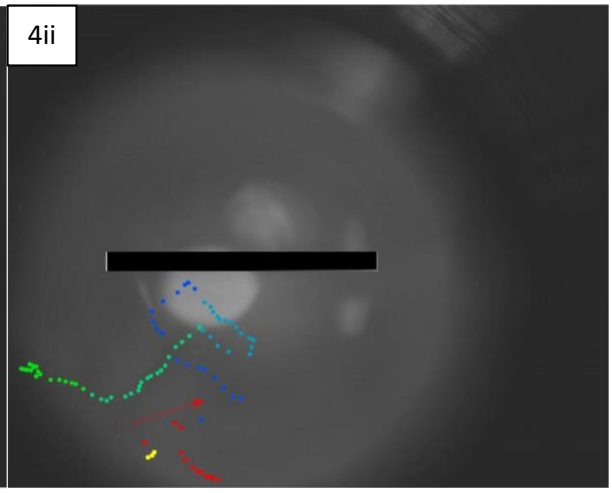
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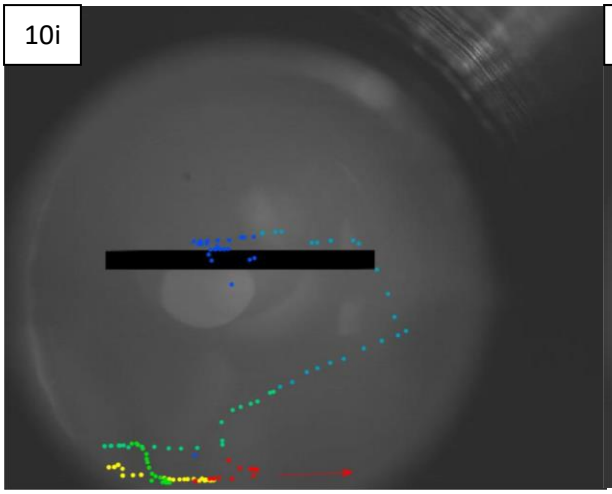
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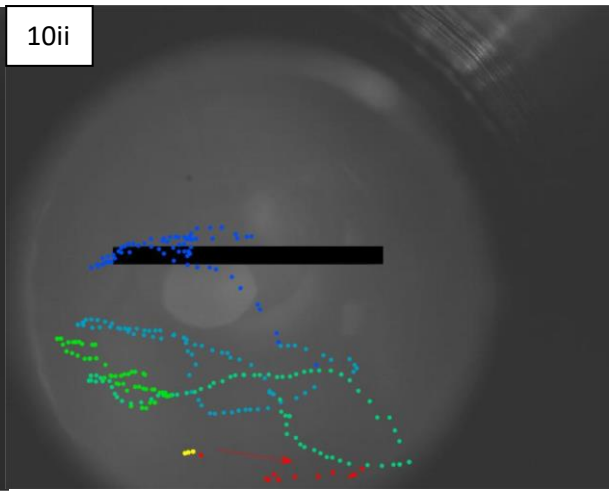
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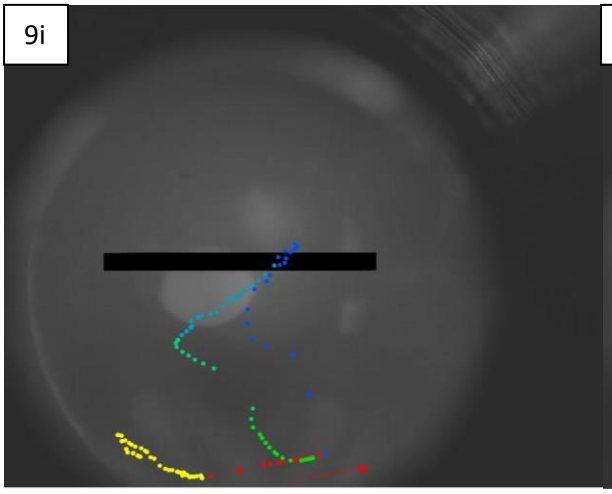
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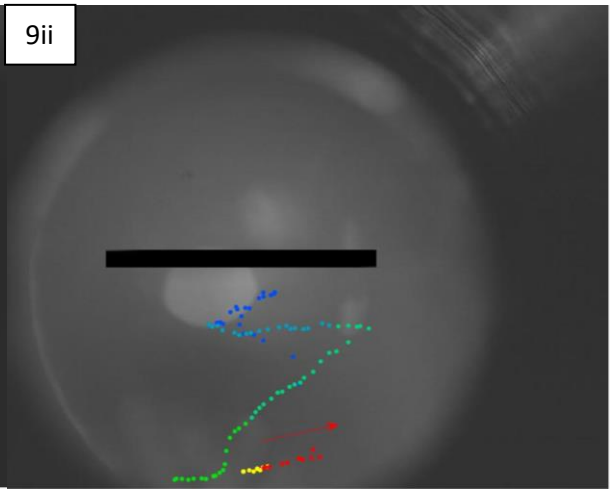
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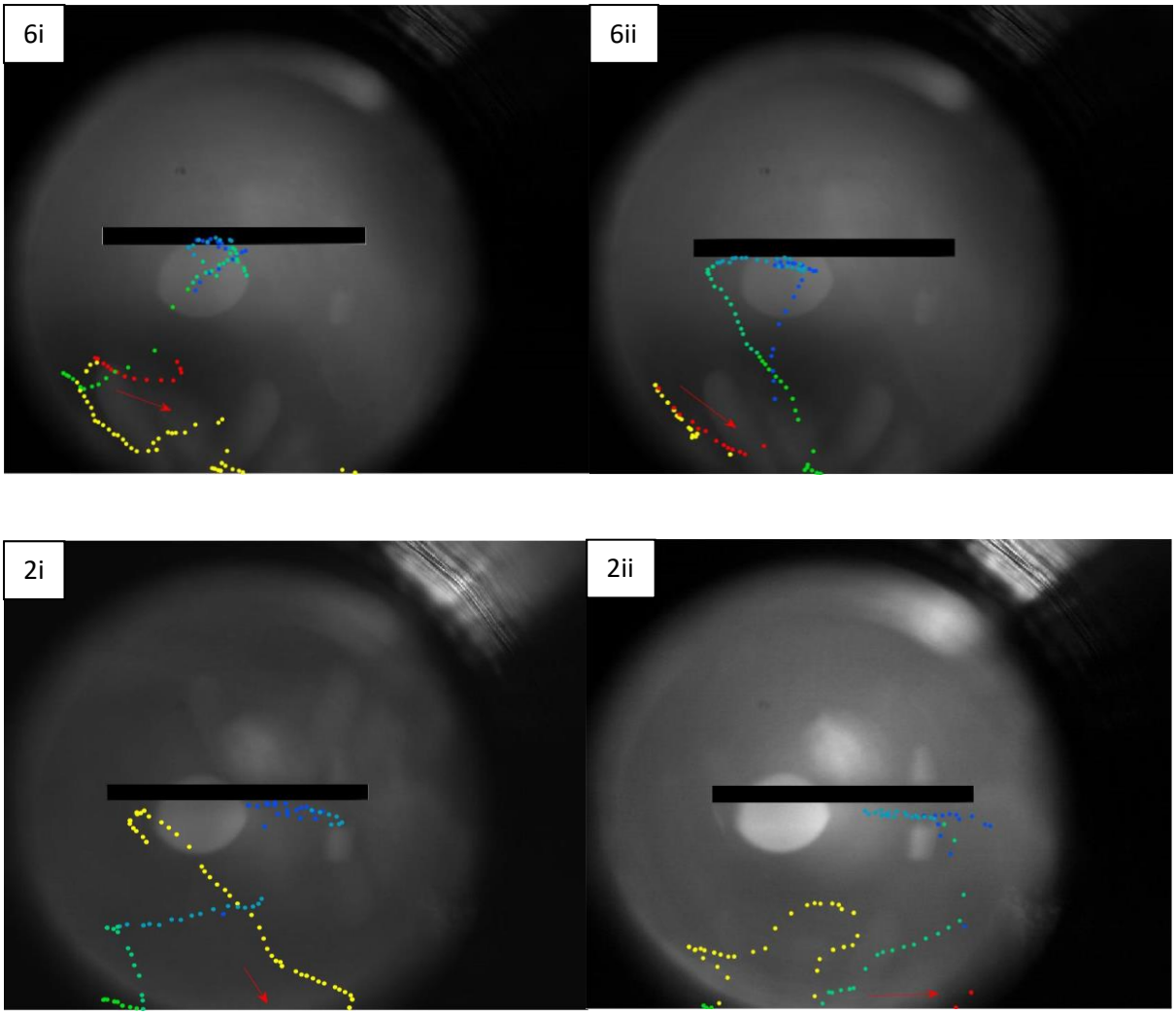
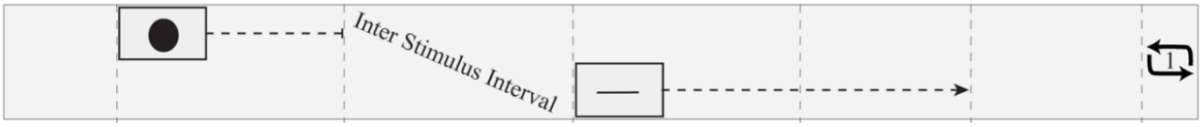
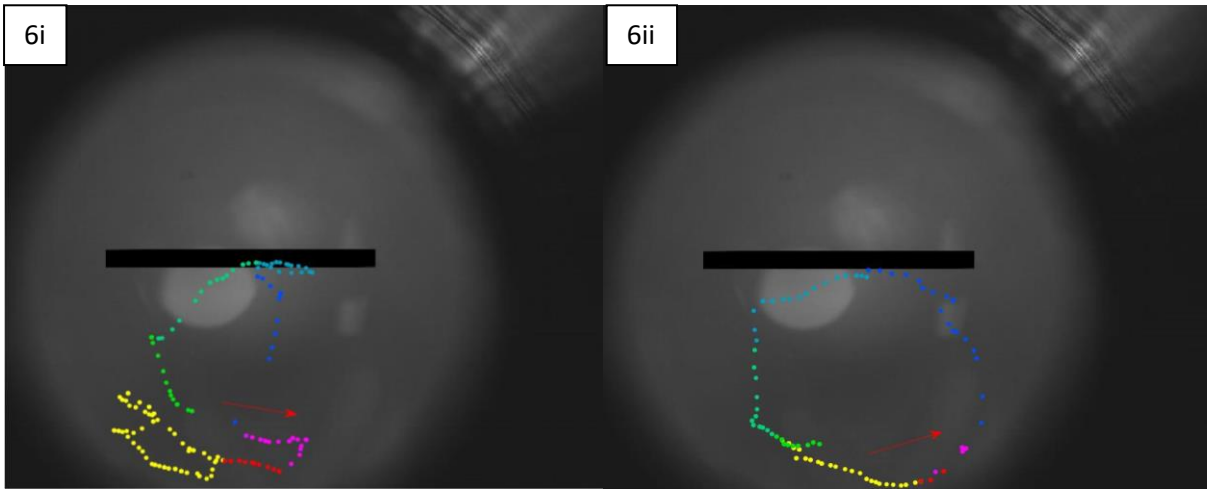
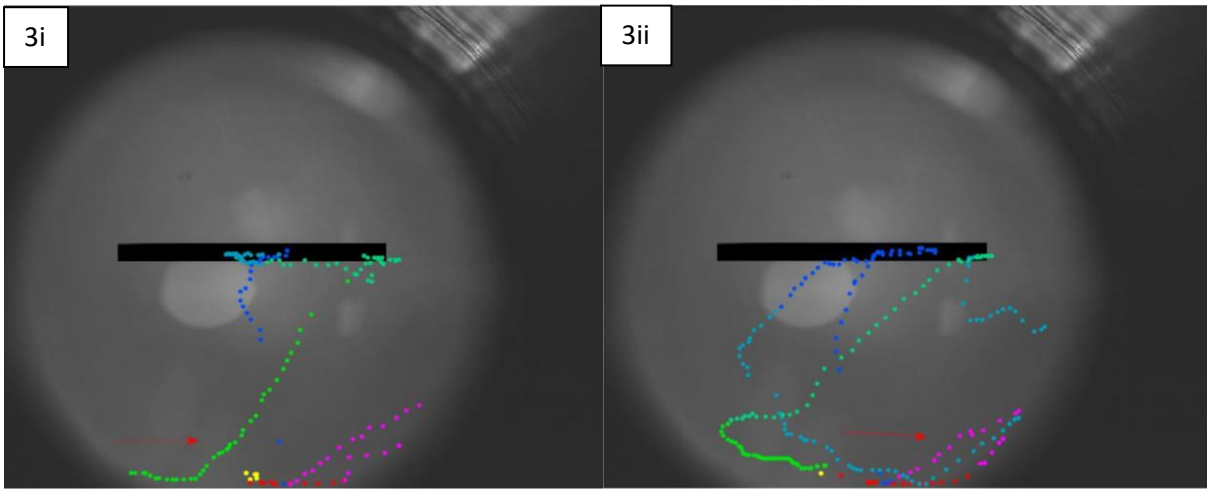


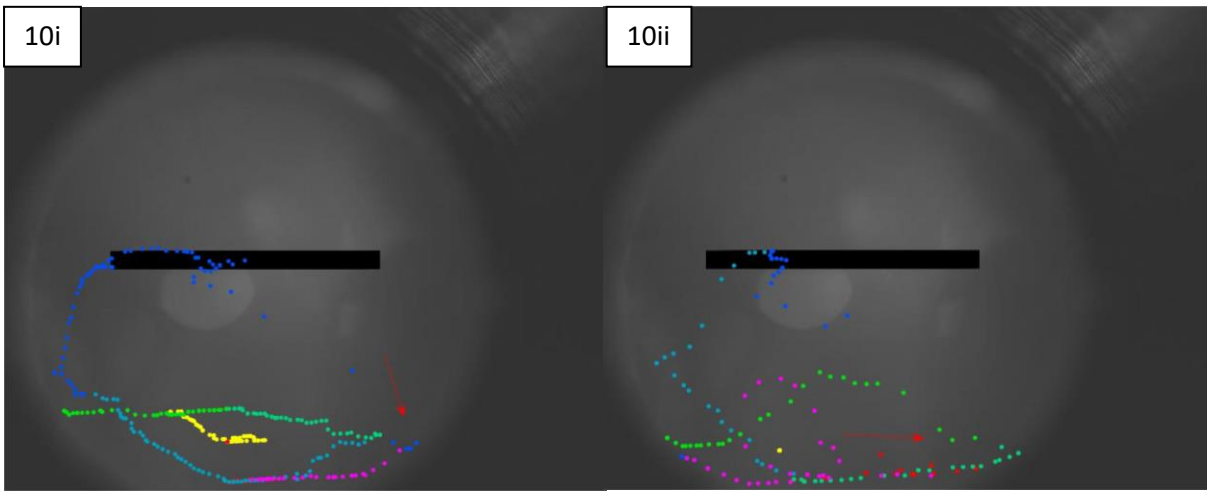
Figure 2. Track from the primary retina in response to the circle-bar priming paradigm. Only the track from the left retina is shown. Each point refers to the centre of the retina. Yellow: spontaneous activity, prior to presentation of stimuli. Red: Movement during the priming stimulus; Red arrow shows the initial direction of the saccade. Blue to green: pattern of scanning during the presentation of the main stimulus. Main stimulus is superimposed onto the image for reference. Plots are ordered in clarity, from the tracks with the strongest priming effect to the least. Numbers 1-11 indicate the spider identification number. i. Iteration 1. ii. Iteration 2.

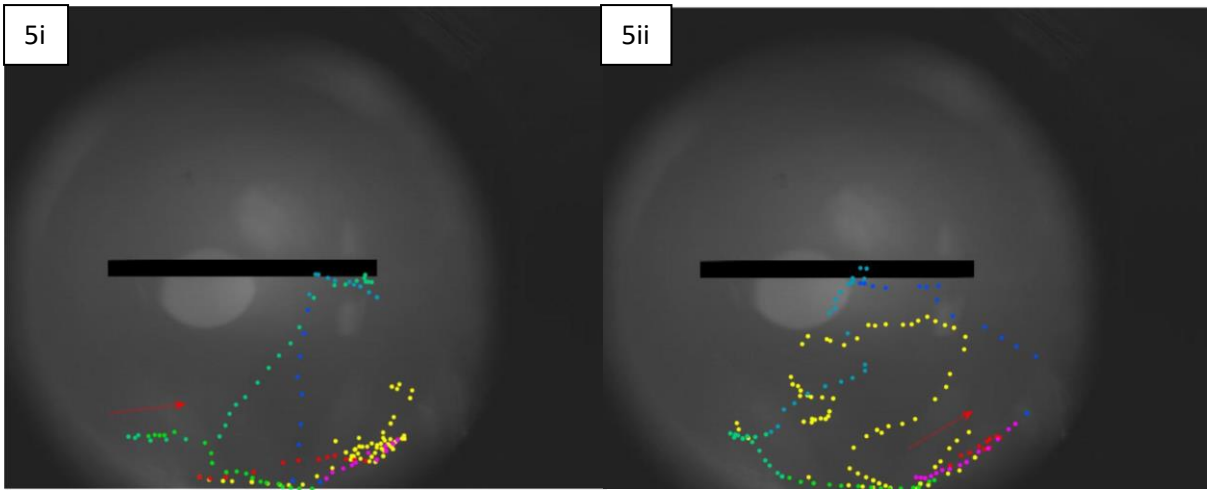
Circle-Bar Delay Tracks







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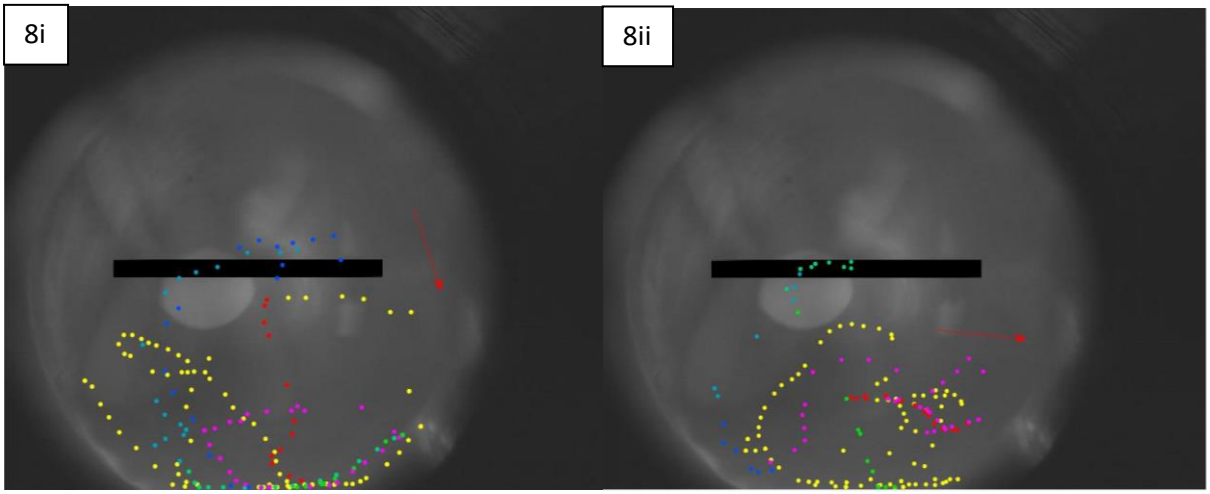
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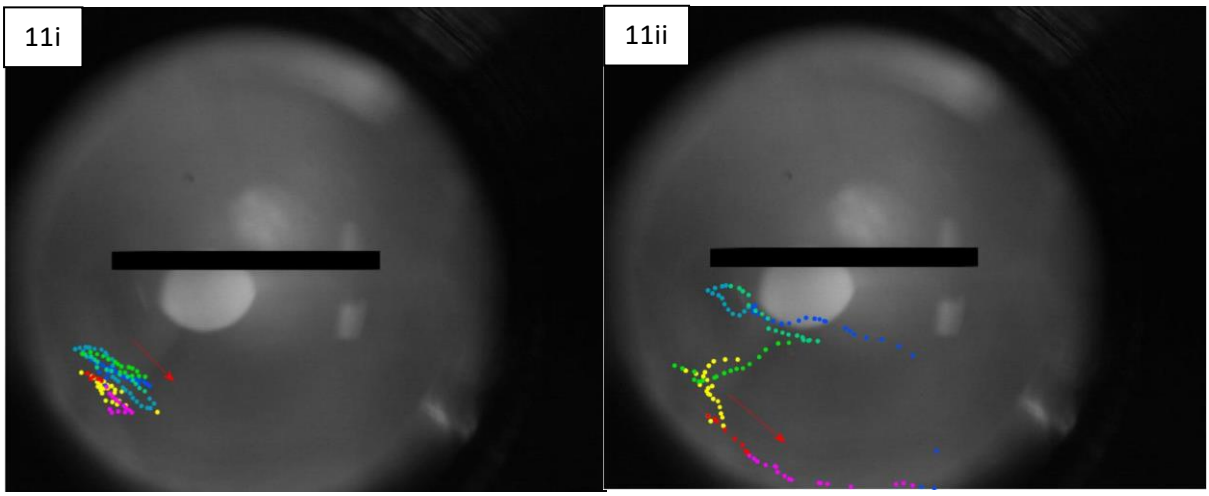
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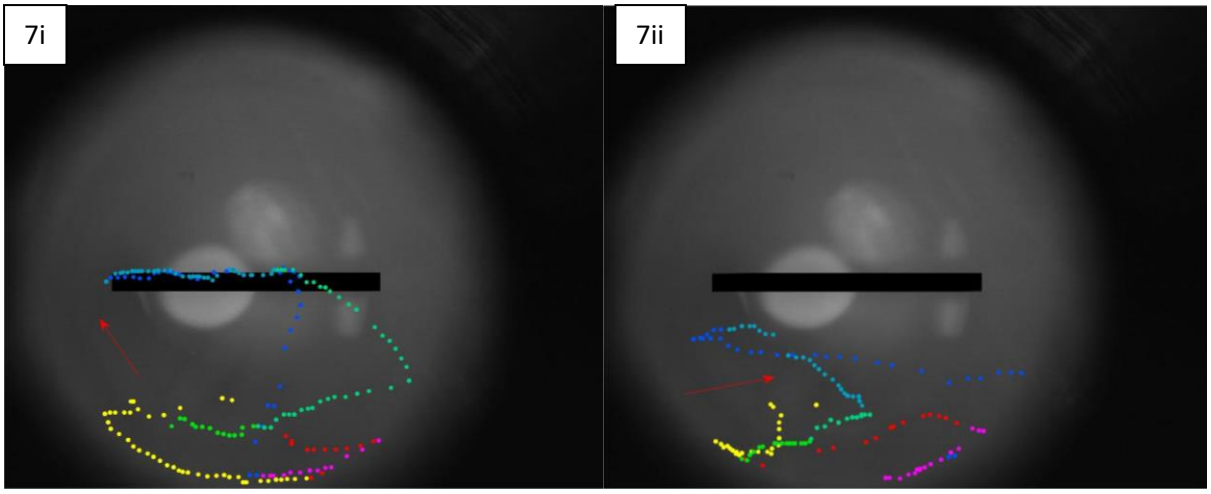
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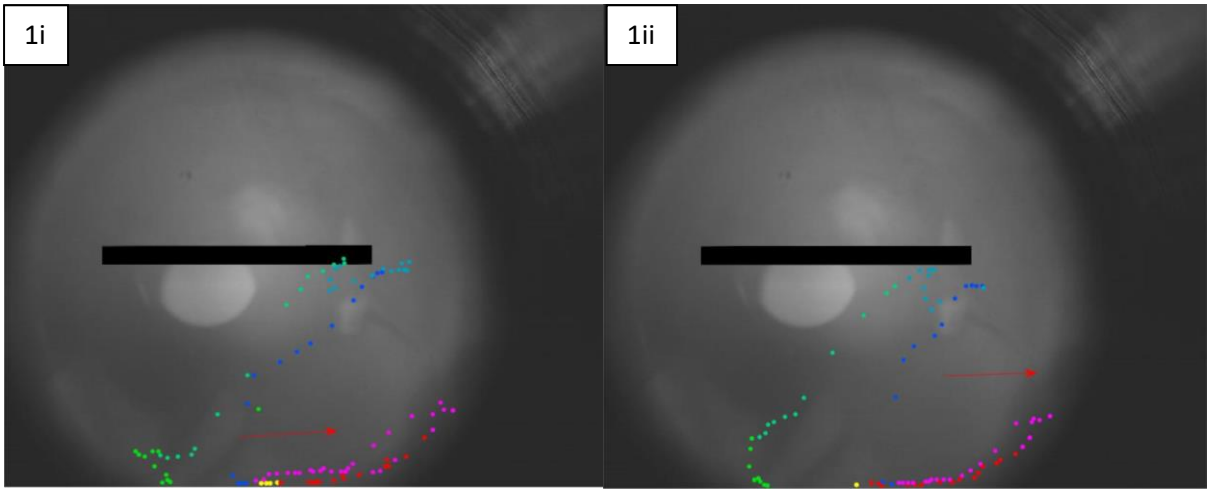
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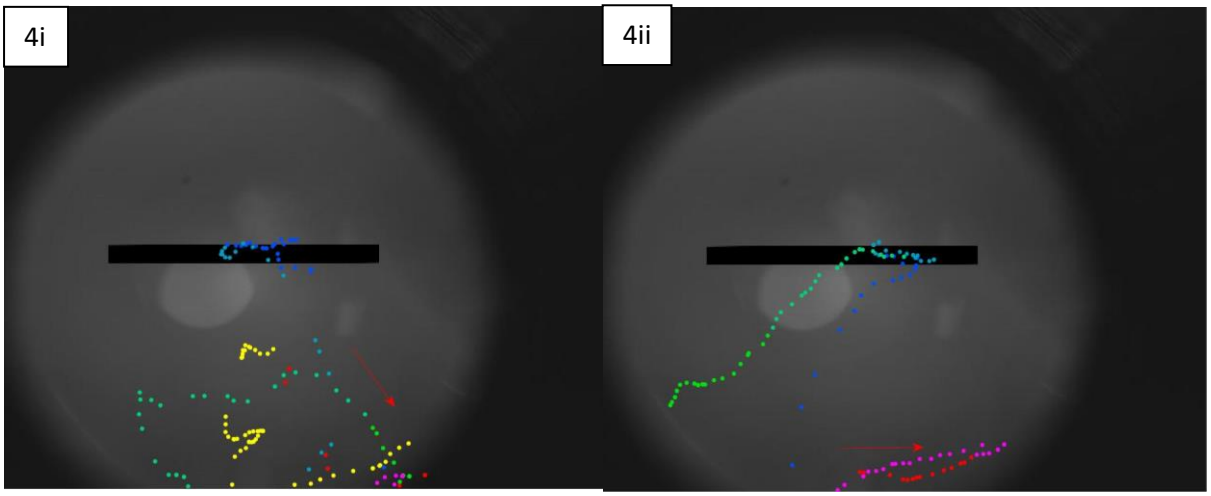
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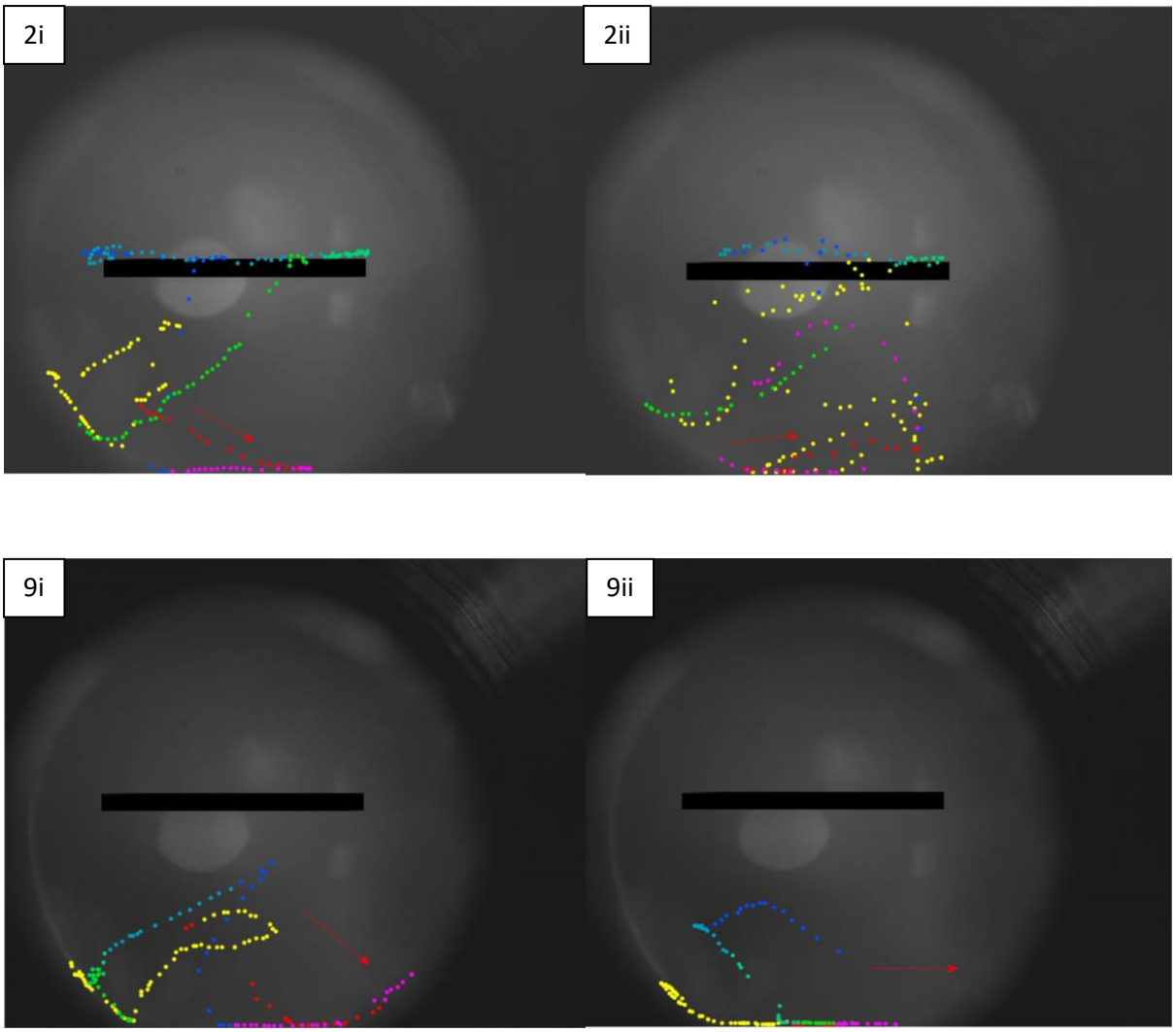
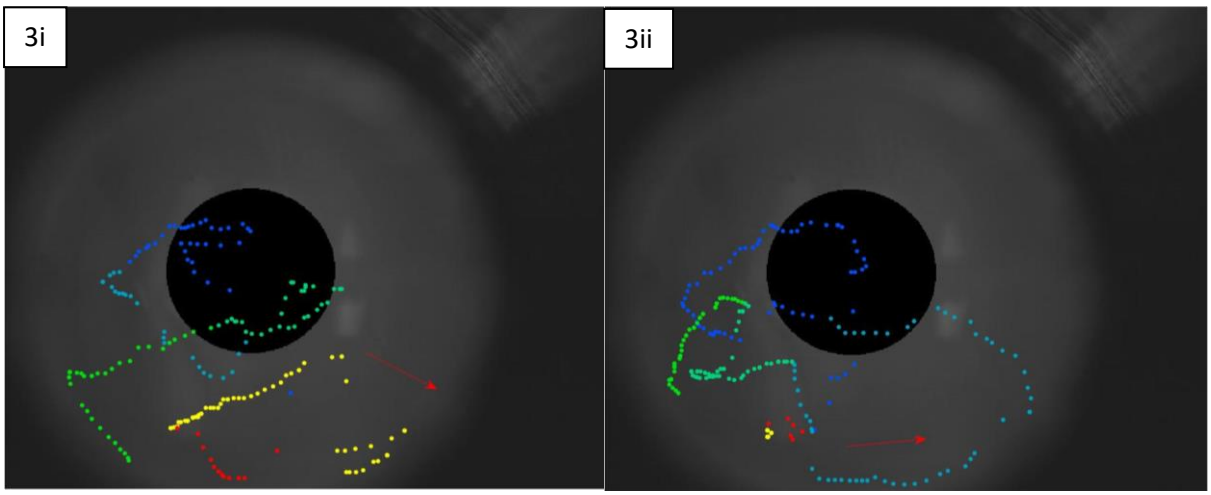
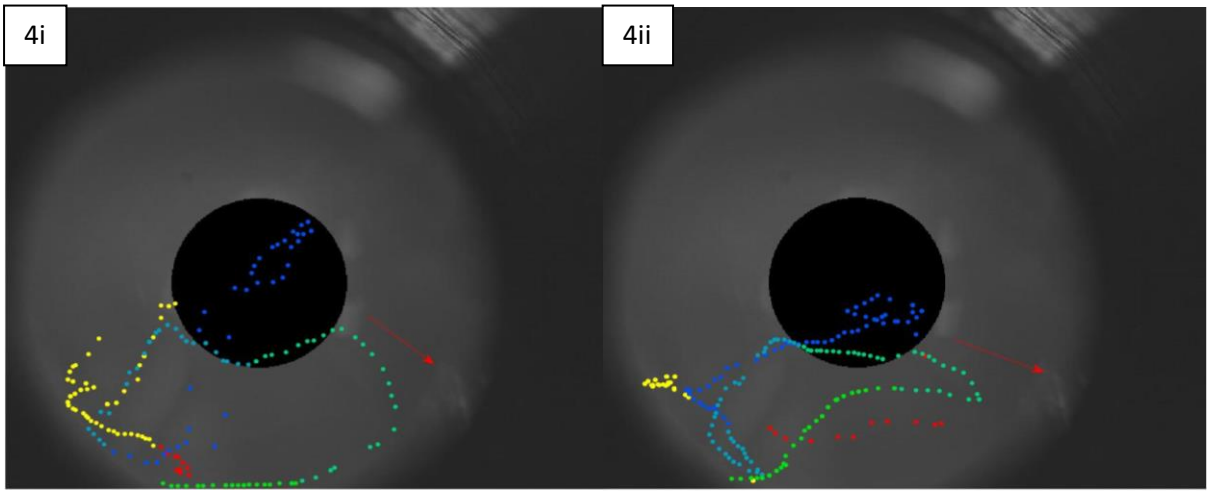
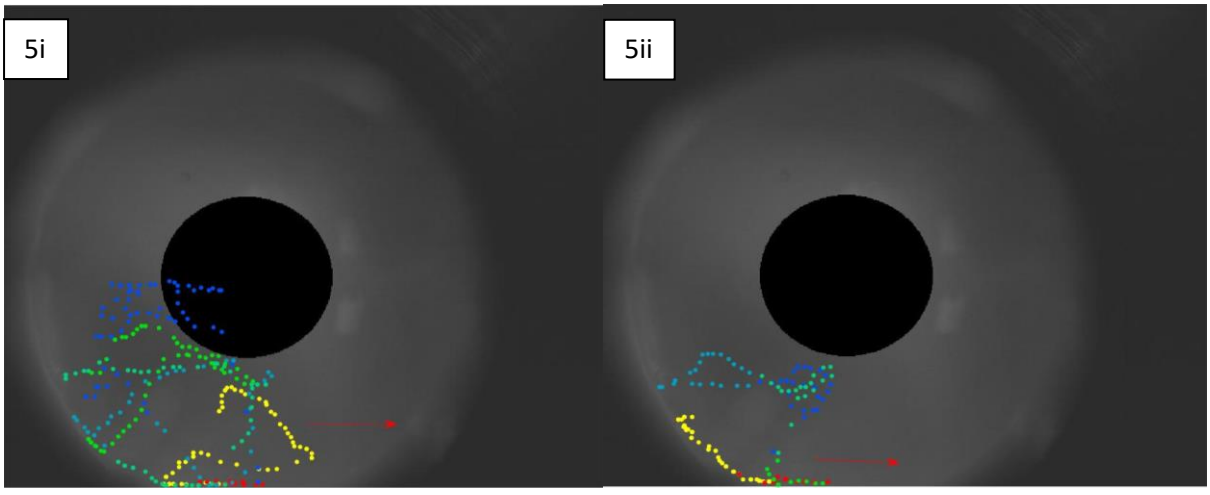


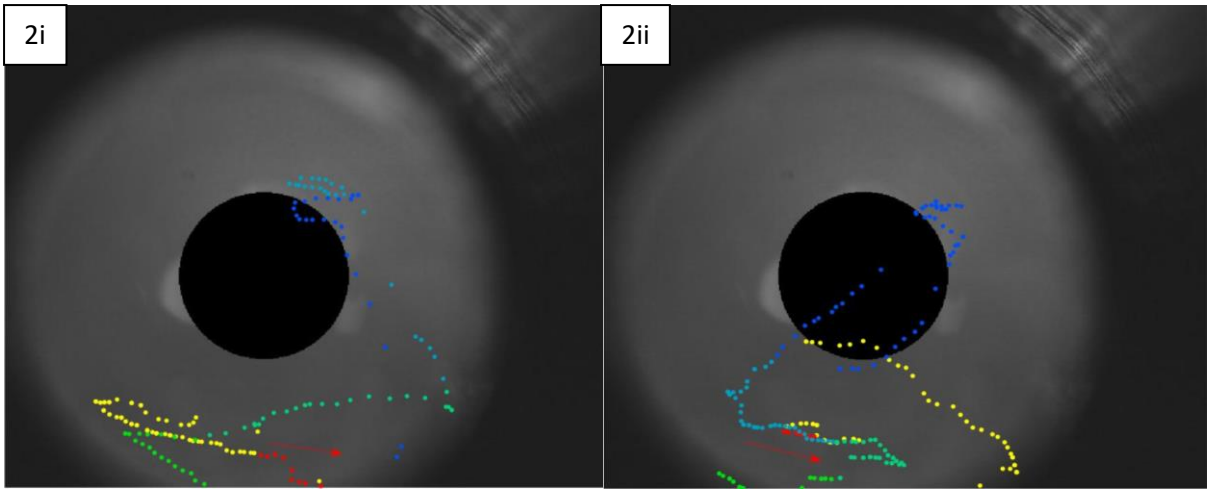
Figure 3. Track from the primary retina in response to the circle-bar delay priming paradigm. Only the track from the left retina is shown. Each point refers to the centre of the retina. Yellow: spontaneous activity, prior to presentation of stimuli. Red: Movement during the priming stimulus; Red arrow shows the initial direction of the saccade. Purple: Inter-stimulus delay. Blue to green: pattern of scanning during the presentation of the main stimulus. Main stimulus is superimposed onto the image for reference. Plots are ordered in clarity, from the tracks with the strongest priming effect to the least. Numbers 1-11 indicate the spider identification number. i. Iteration 1. ii. Iteration 2.

Circle-Circle Tracks





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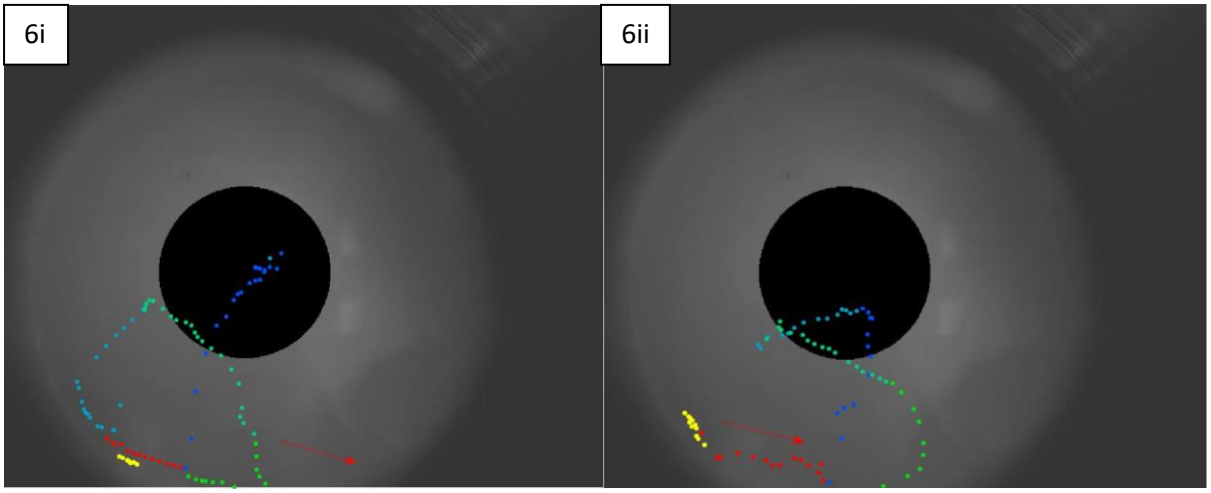
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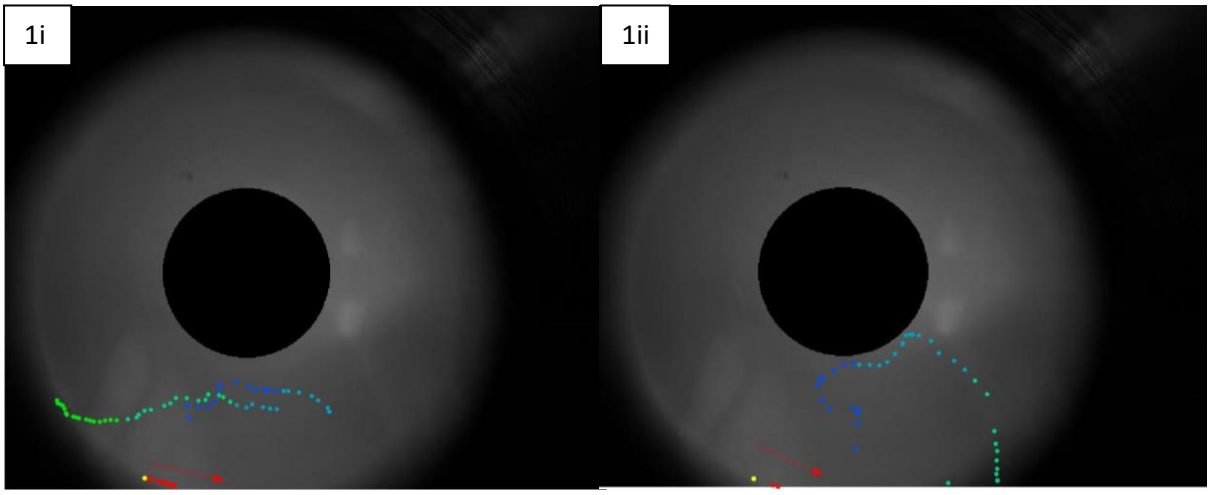
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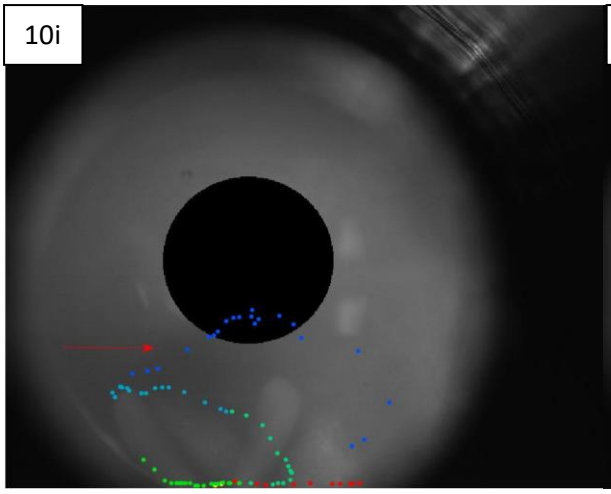
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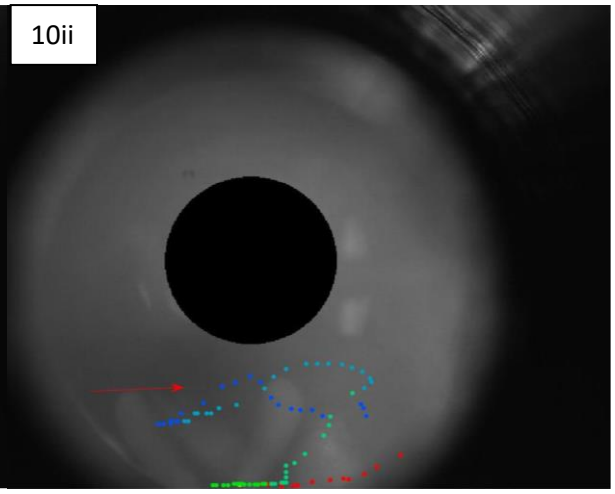
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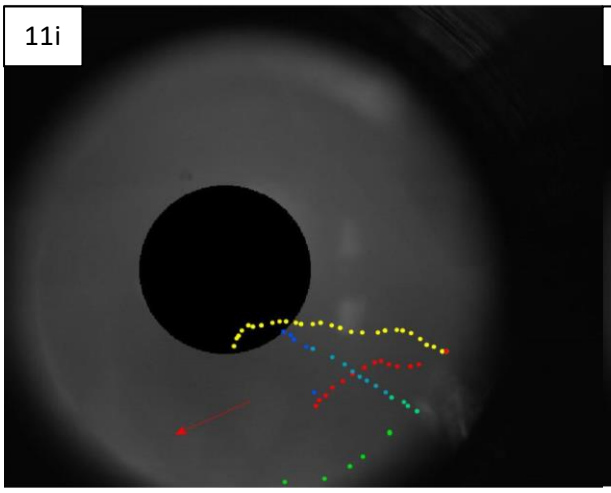
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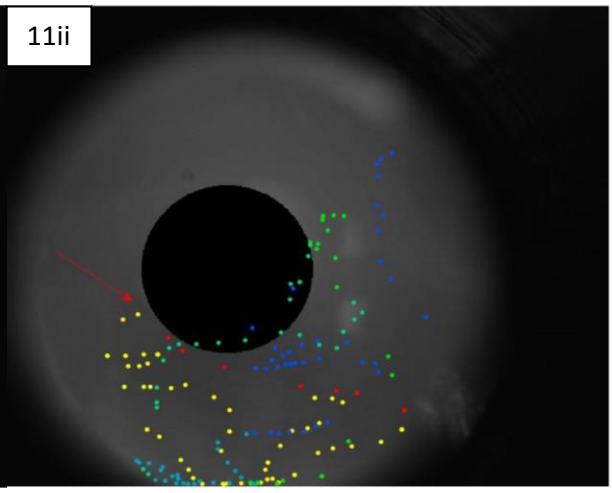
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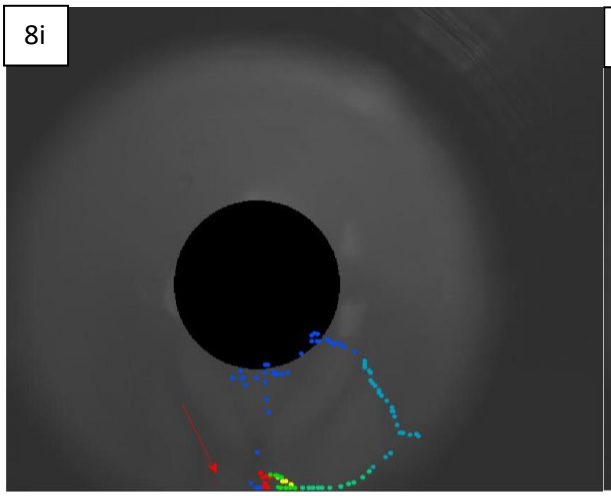
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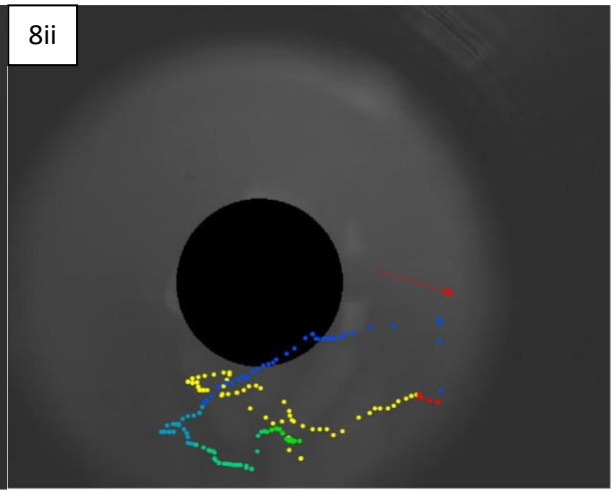
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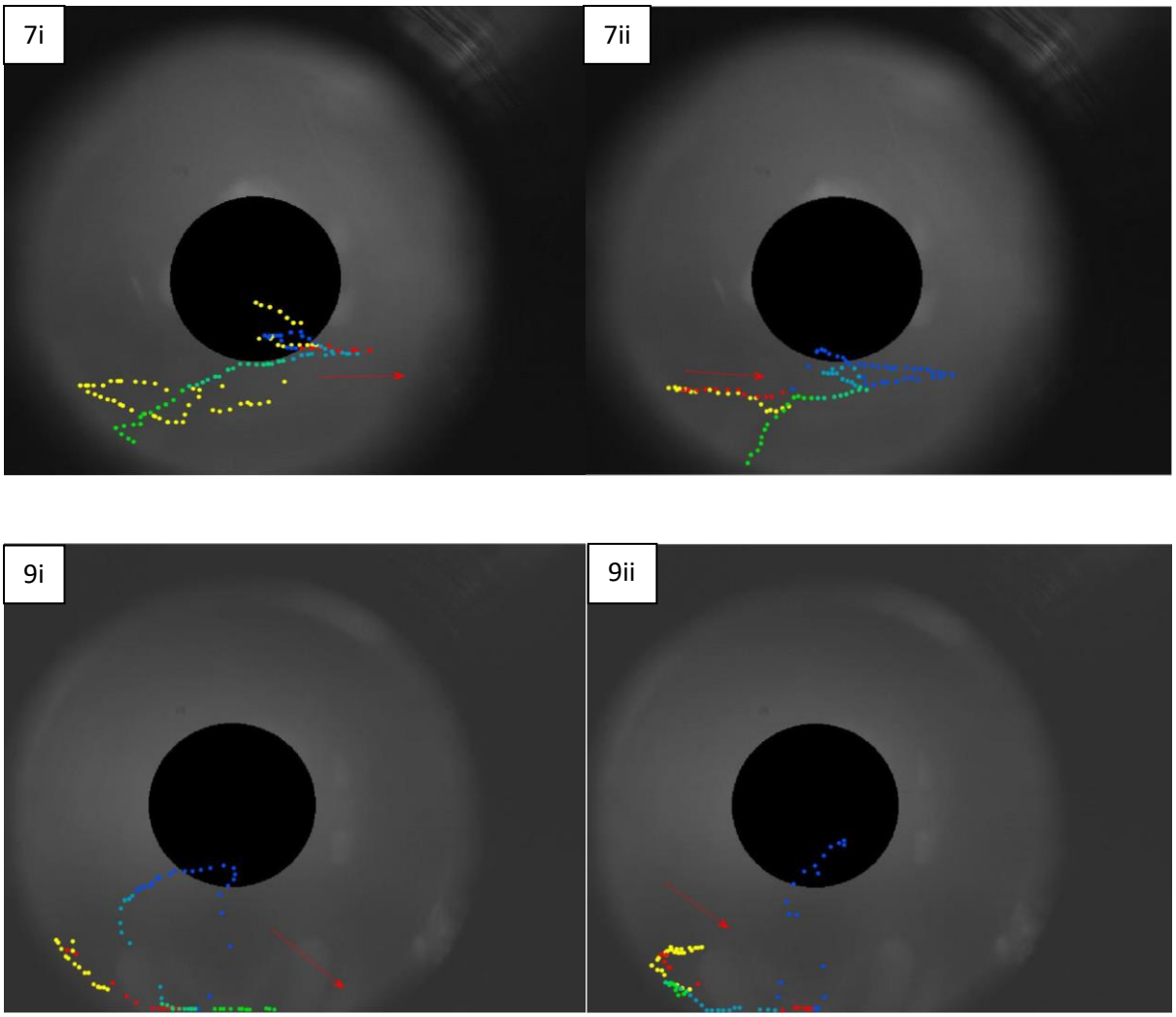
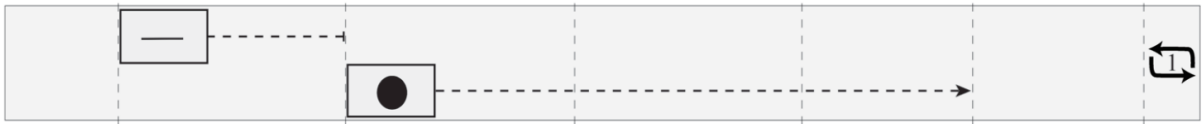
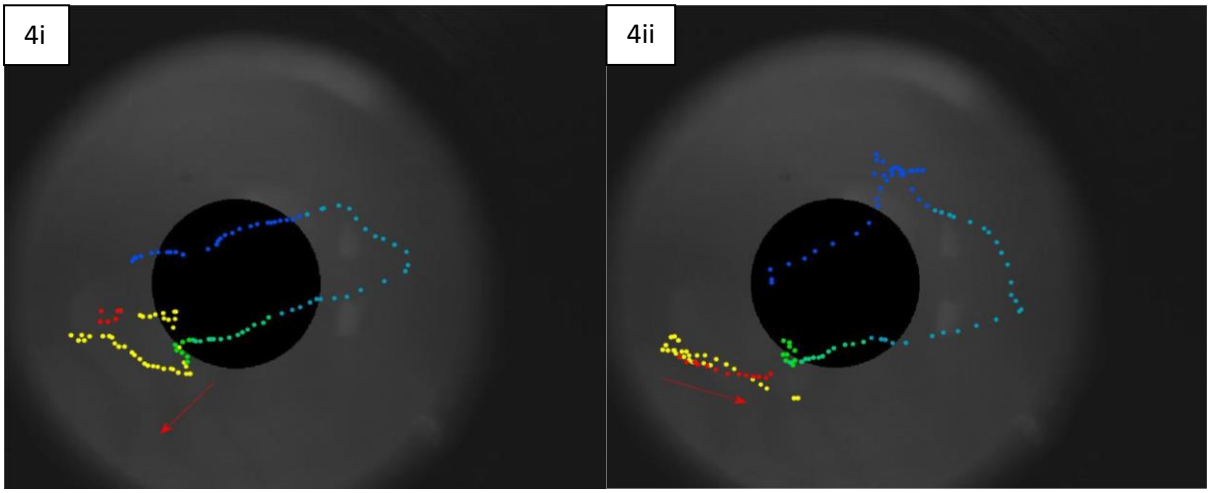
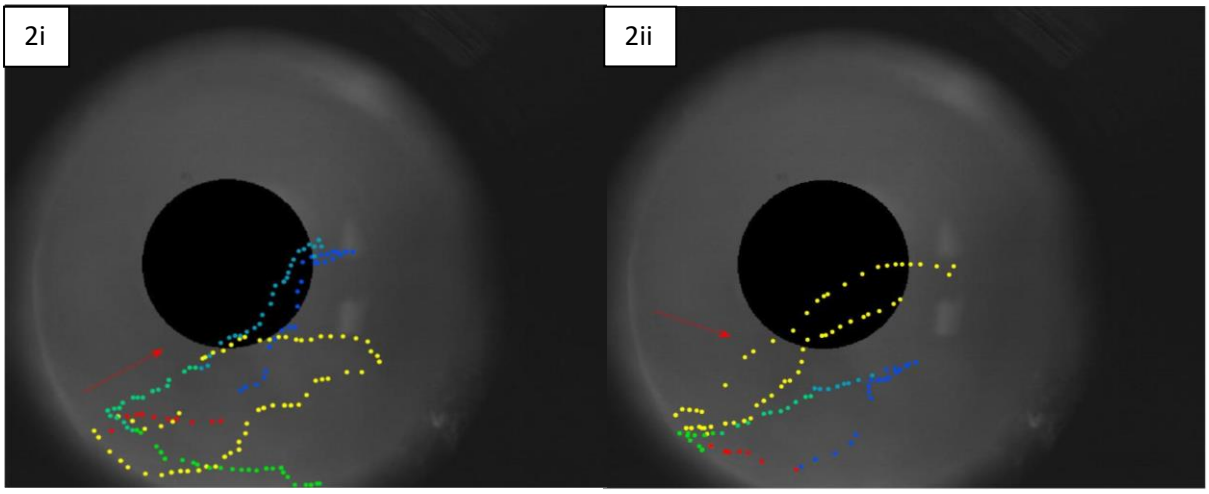


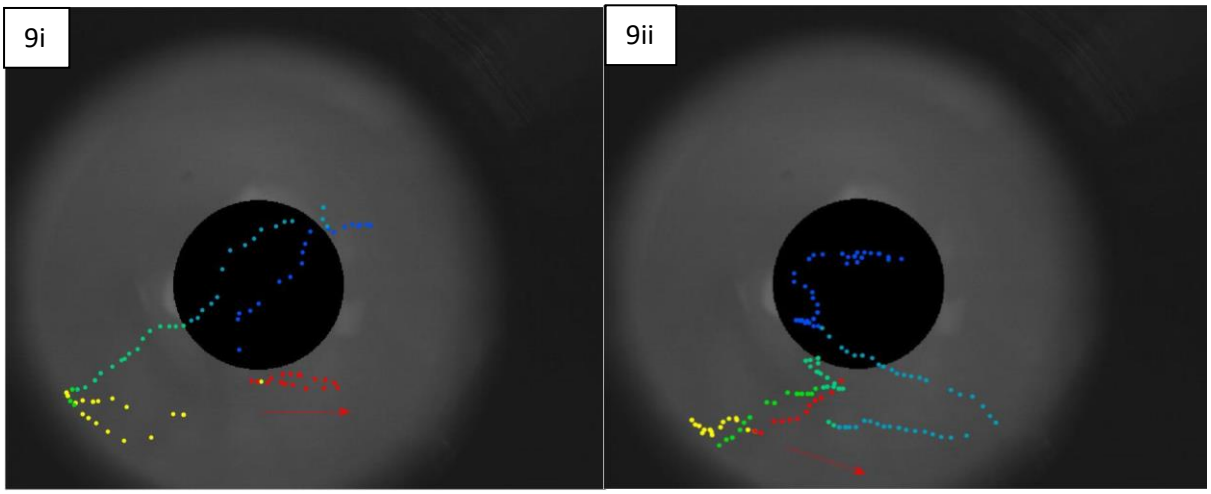
Figure 4. Track from the primary retina in response to the circle-circle priming paradigm. Only the track from the left retina is shown. Each point refers to the centre of the retina. Yellow: spontaneous activity, prior to presentation of stimuli. Red: Movement during the priming stimulus; Red arrow shows the initial direction of the saccade. Blue to green: pattern of scanning during the presentation of the main stimulus. Main stimulus is superimposed onto the image for reference. Plots are ordered in clarity, from the tracks with the most targeted tracking to the least. Numbers 1-11 indicate the spider identification number. i. Iteration 1. ii. Iteration 2.

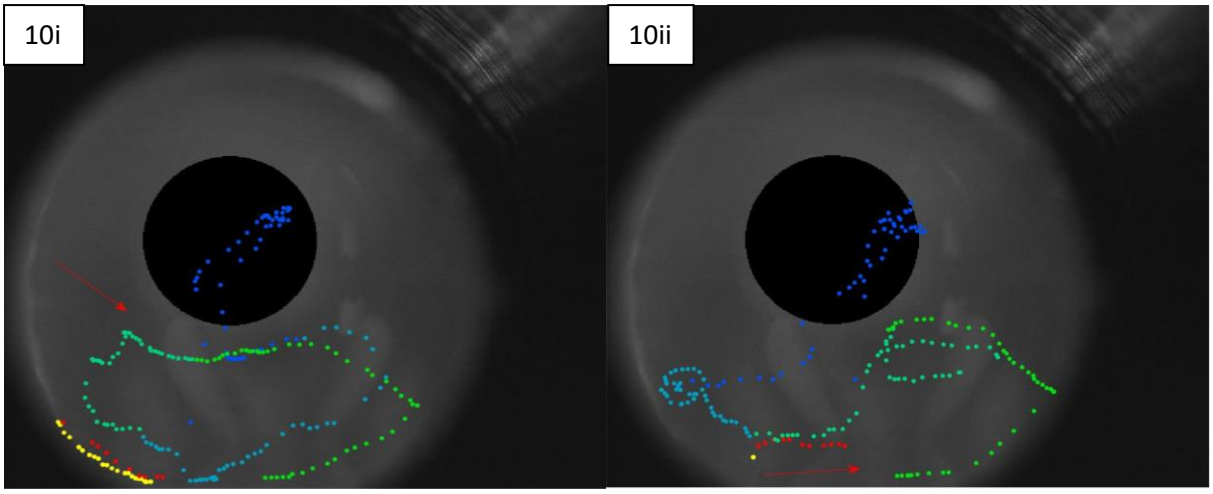
Bar-Circle Tracks







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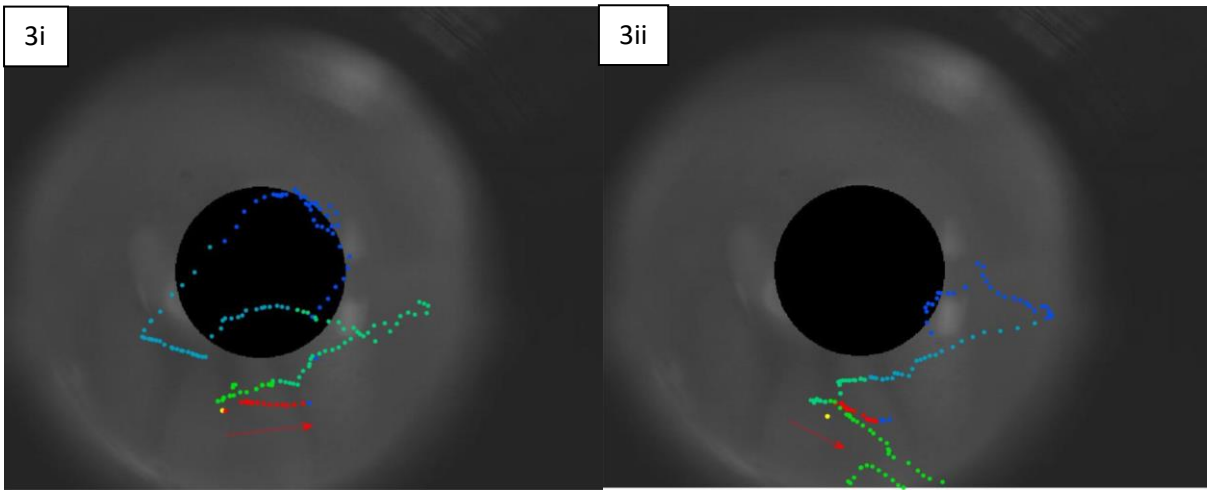
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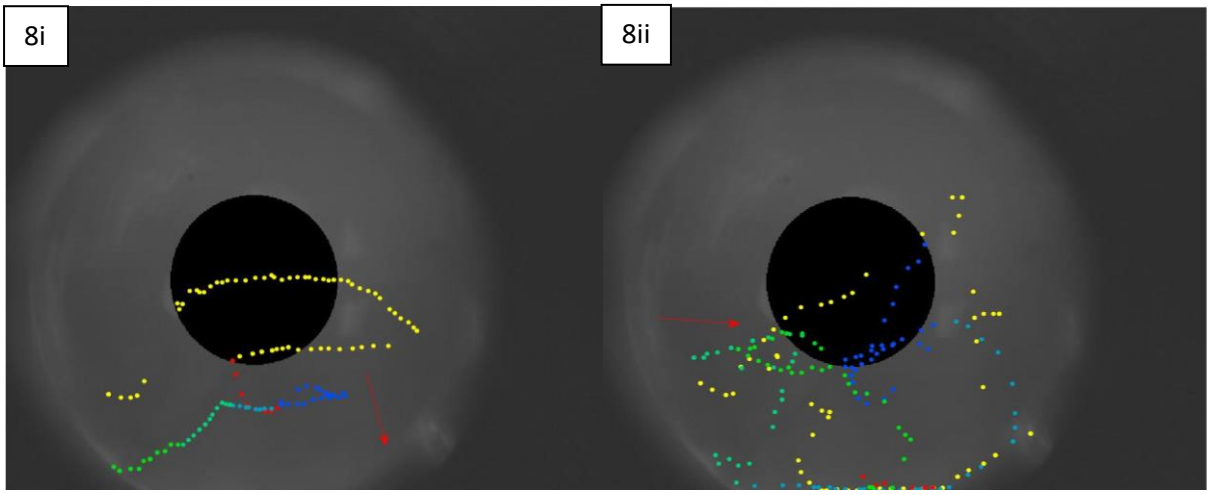
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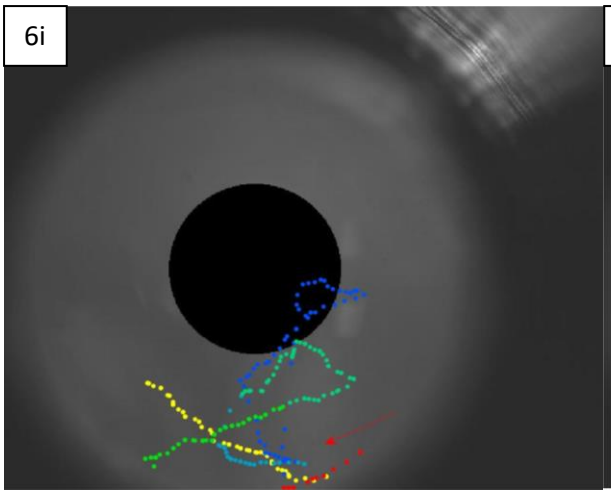
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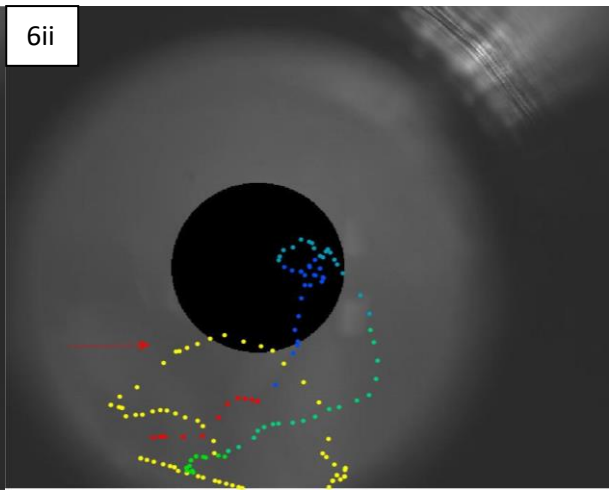
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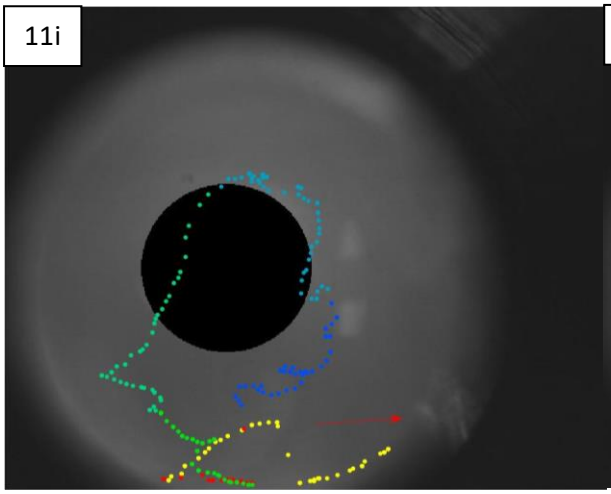
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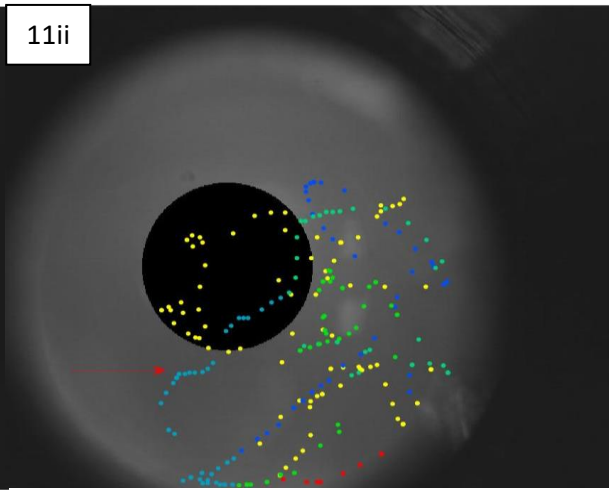
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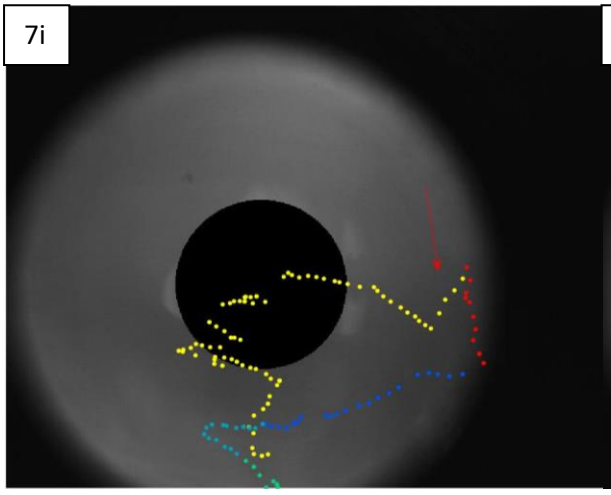
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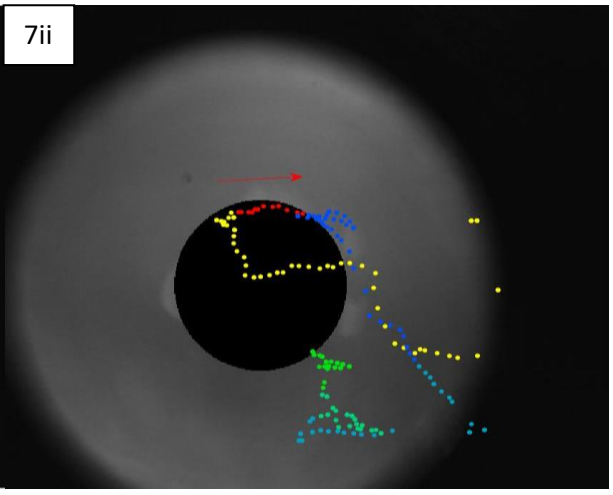
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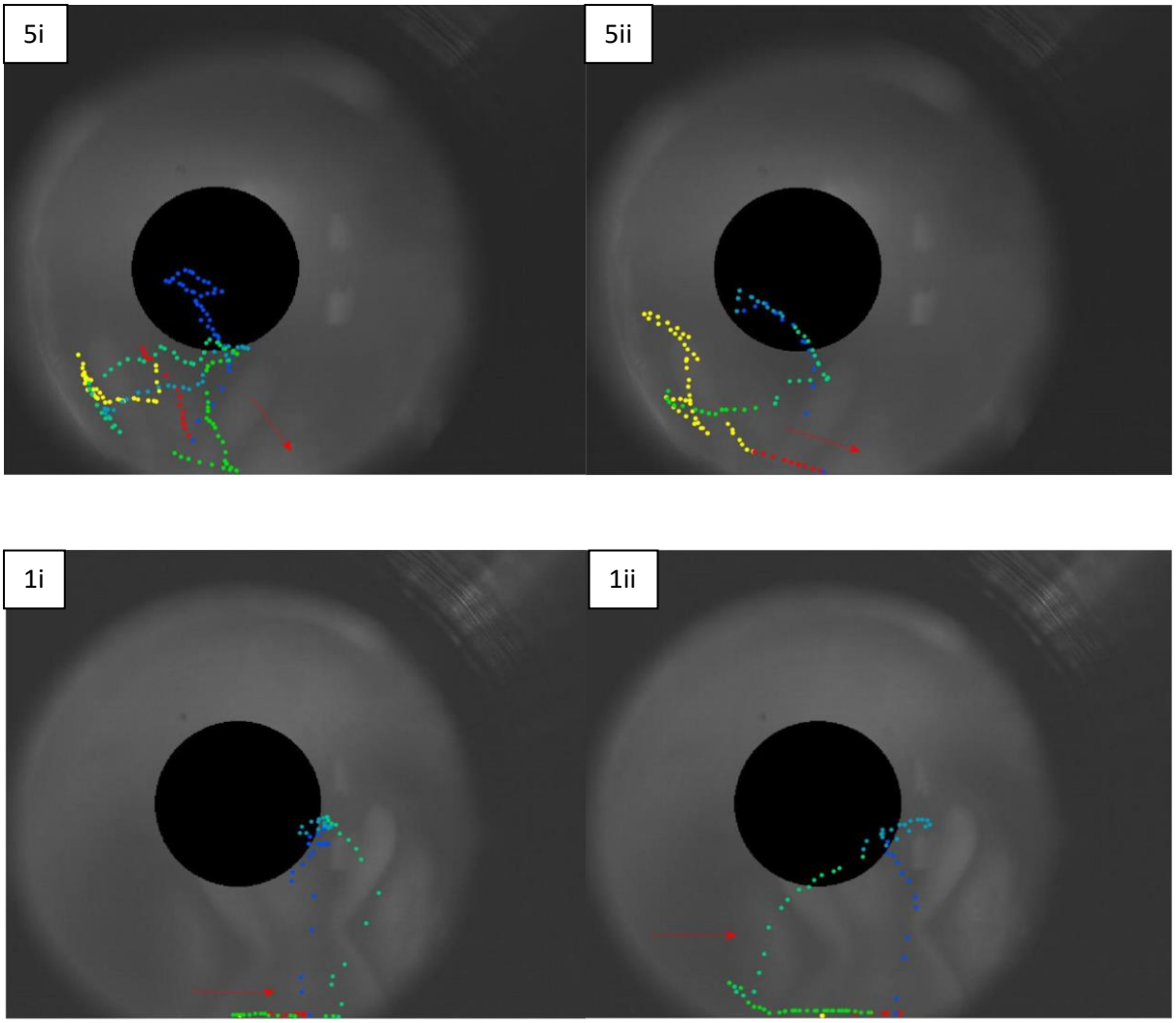
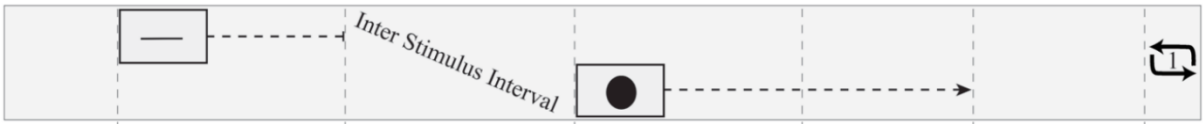
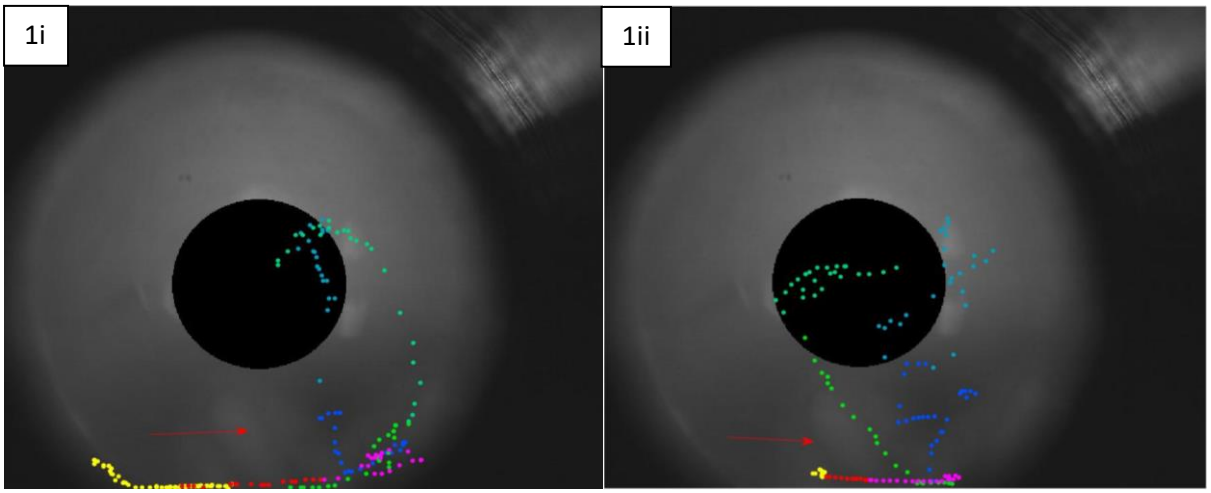
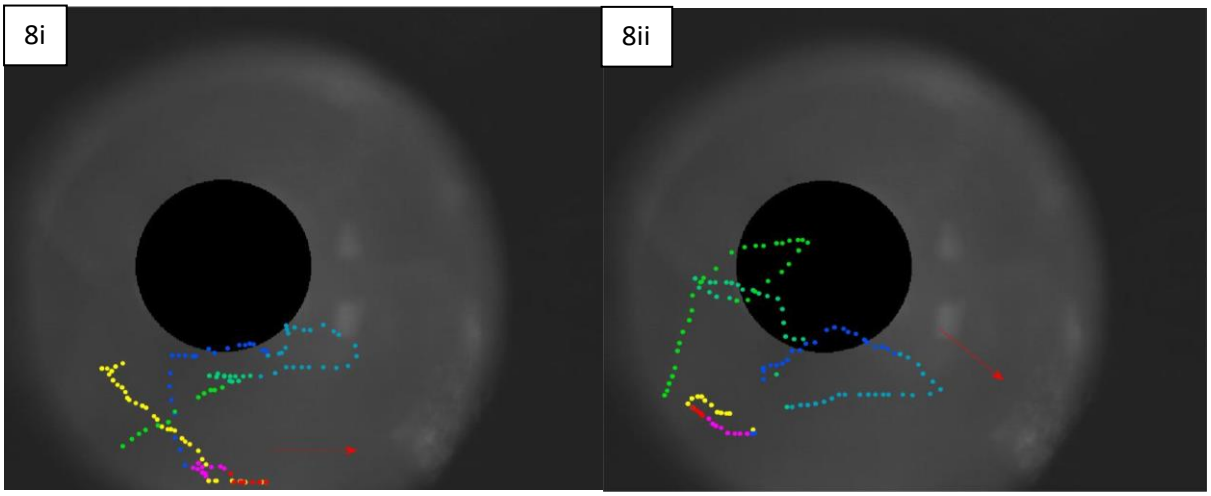


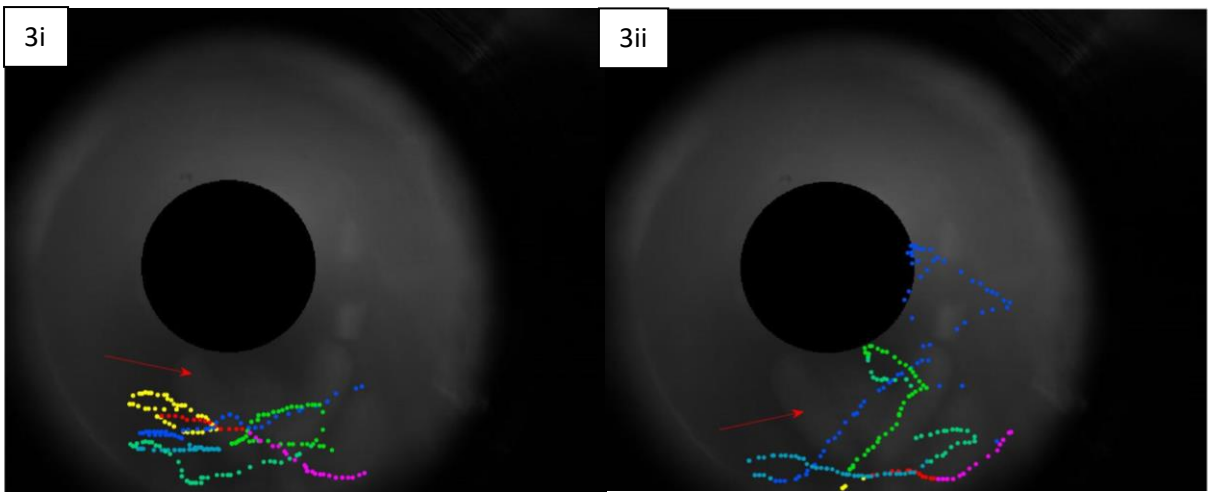
Figure 5. Track from the primary retina in response to the bar-circle priming paradigm. Only the track from the left retina is shown. Each point refers to the centre of the retina. Yellow: spontaneous activity, prior to presentation of stimuli. Red: Movement during the priming stimulus; Red arrow shows the initial direction of the saccade. Blue to green: pattern of scanning during the presentation of the main stimulus. Main stimulus is superimposed onto the image for reference. Plots are ordered in clarity, from the tracks with the strongest priming effect to the least. Numbers 1-11 indicate the spider identification number. i. Iteration 1. ii. Iteration 2.

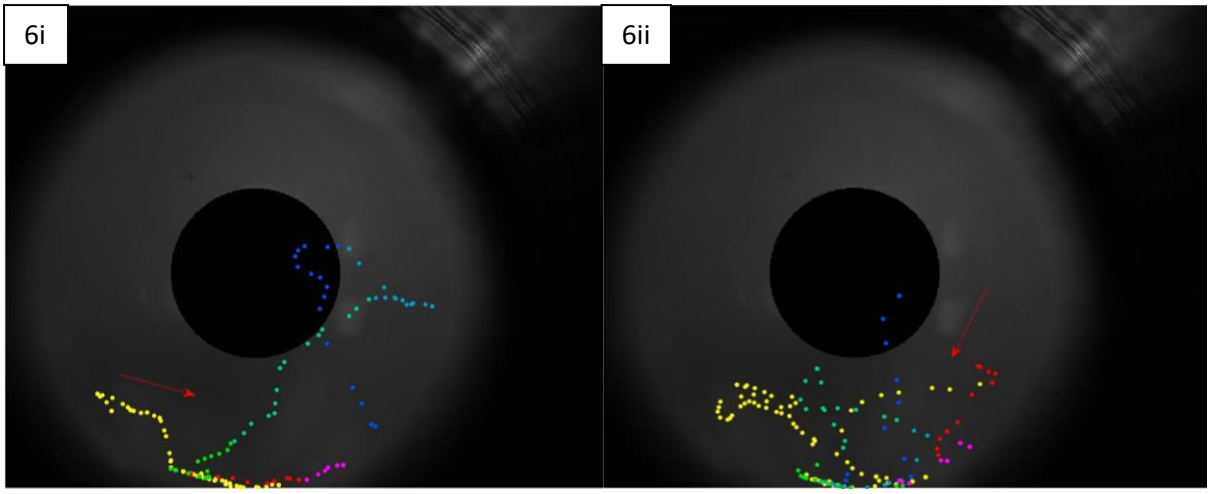
Bar-Circle Delay Tracks







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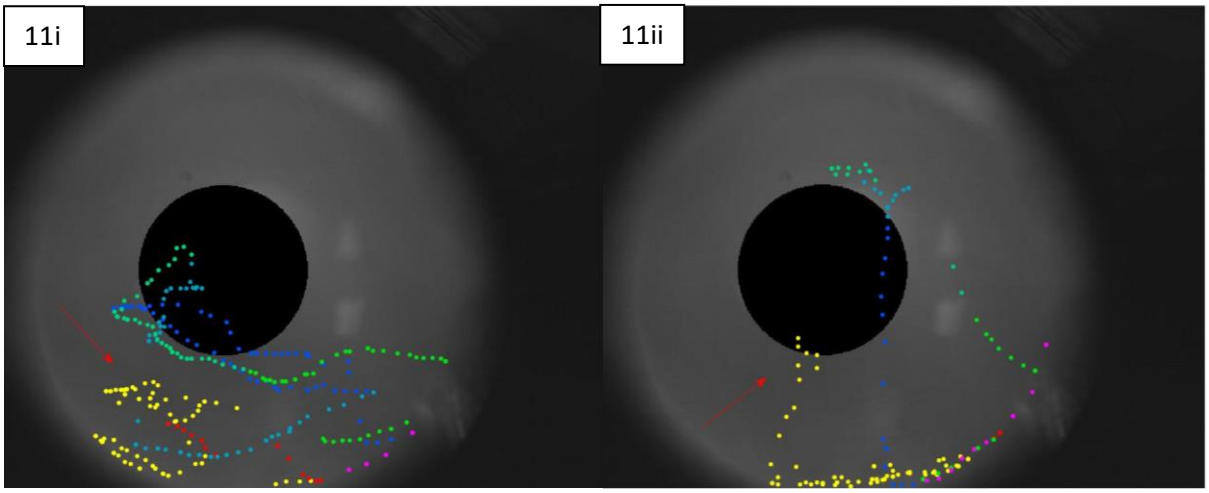
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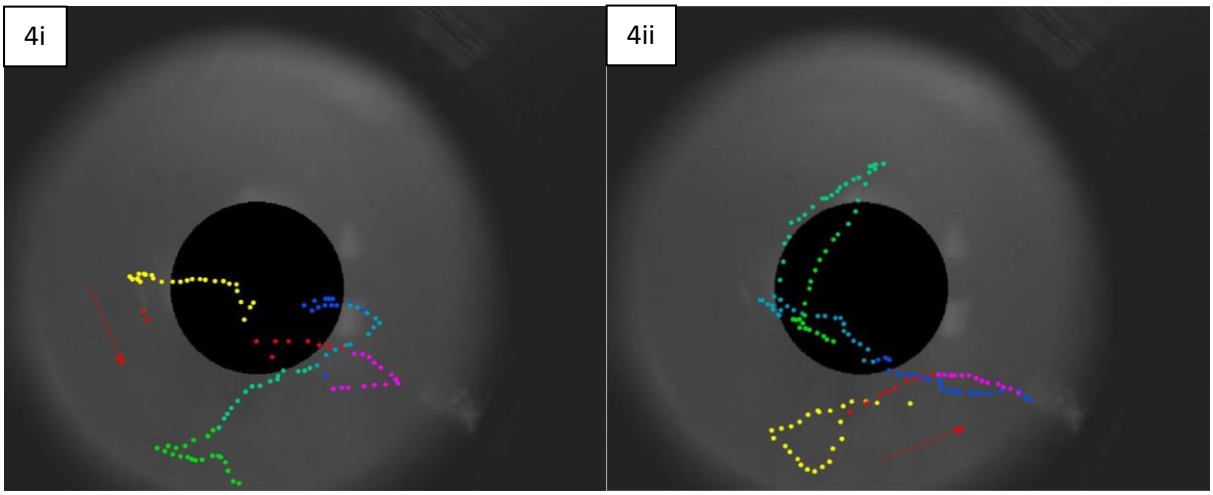
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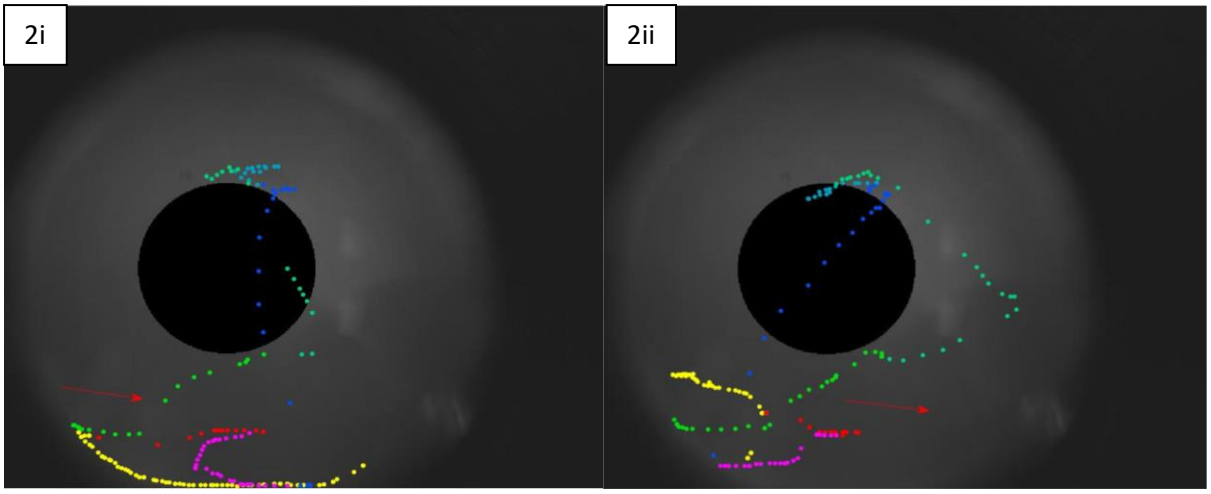
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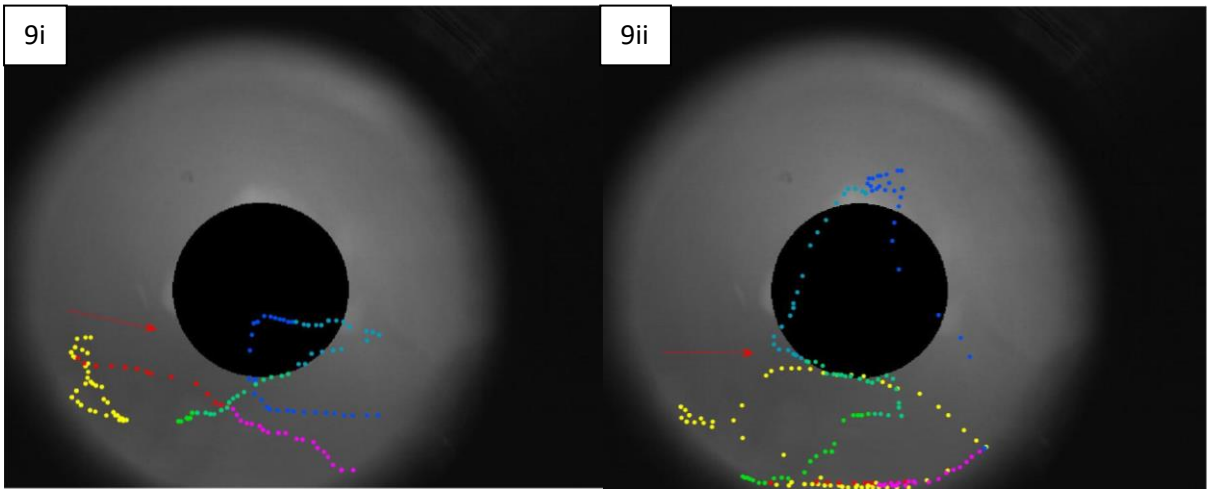
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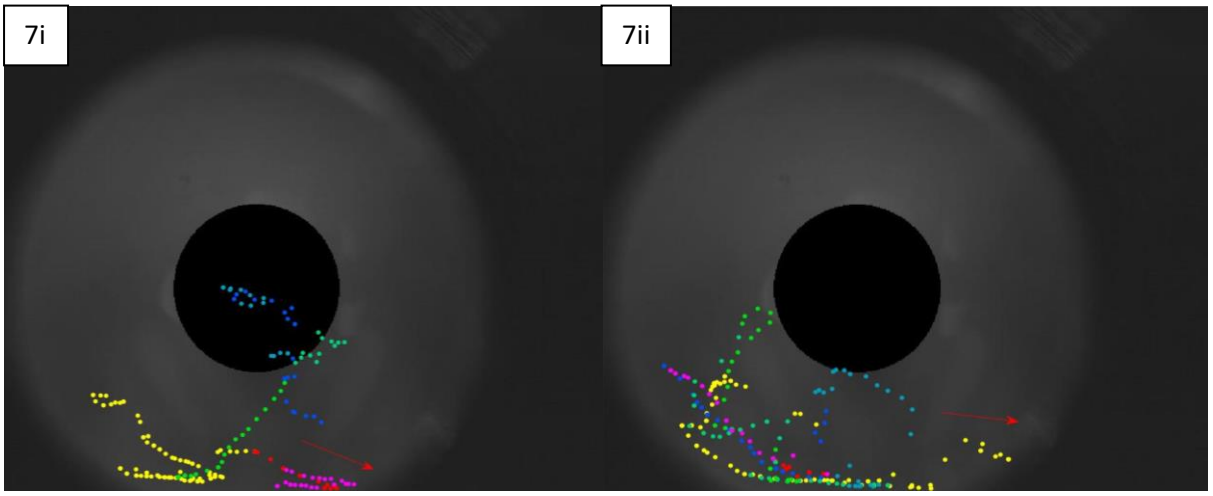
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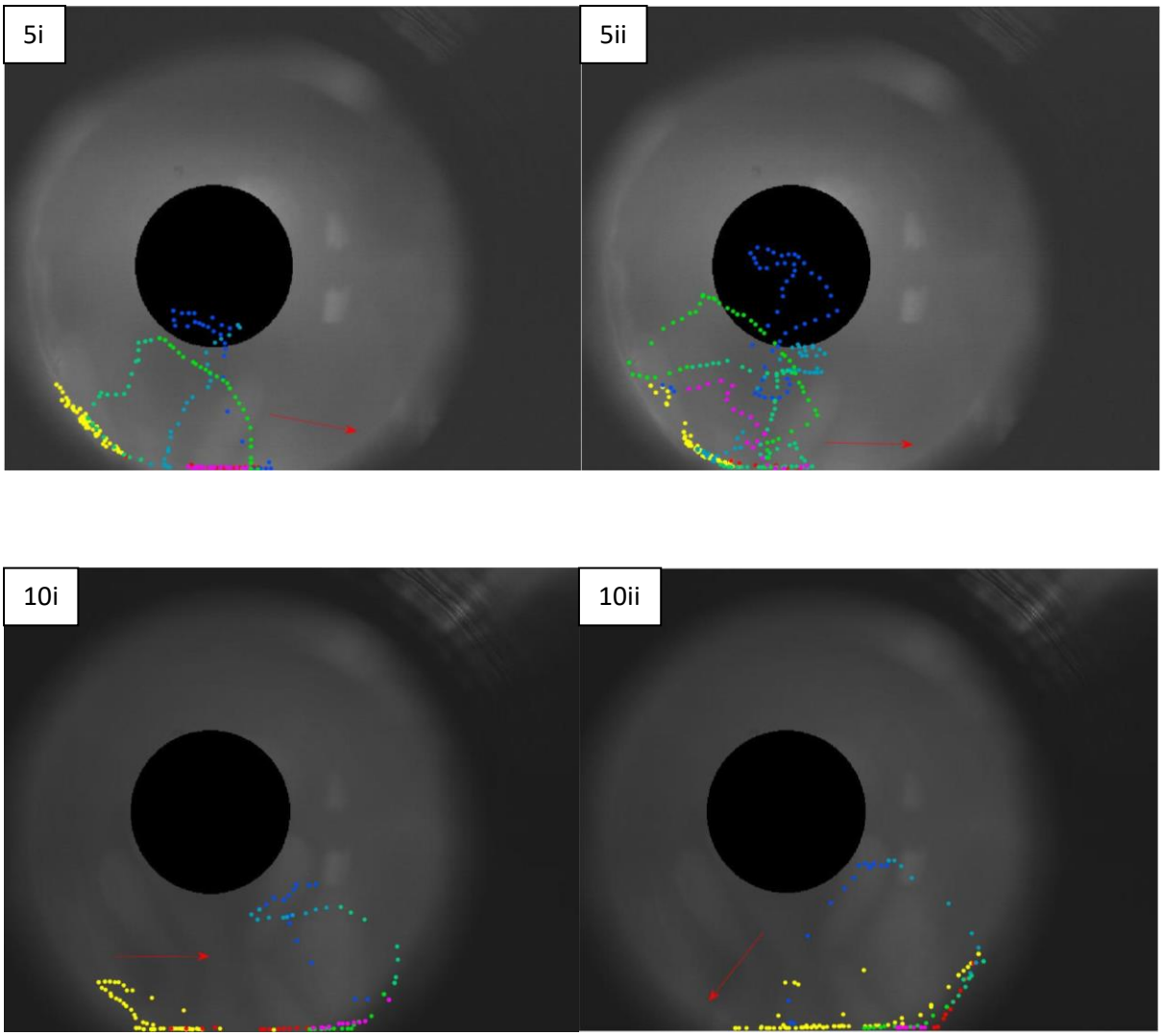

Figure 6. Track from the primary retina in response to the bar-circle delay priming paradigm. Only the track from the left retina is shown. Each point refers to the centre of the retina. Yellow: spontaneous activity, prior to presentation of stimuli. Red: Movement during the priming stimulus; Red arrow shows the initial direction of the saccade. Purple: Inter-stimulus delay. Blue to green: pattern of scanning during the presentation of the main stimulus. Main stimulus is superimposed onto the image for reference. Plots are ordered in clarity, from the tracks with the strongest priming effect to the least. Numbers 1-11 indicate the spider identification number. i. Iteration 1. ii. Iteration 2.